NEW GYMNOSPERMS FROM THE TICÓ FLORA, SANTA CRUZ PROVINCE, ARGENTINA

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NEW GYMNOSPERMS FROM THE TICÓ FLORA, SANTA CRUZ PROVINCE, ARGENTINA

BY

By SERGIO ARCHANGELSKY

SYNOPSIS

The Lower Cretaceous plants described here were collected between 1958 and 1963 from different localities on the outcrop of the Baqueró Formation. A new locality, Bajo Grande, yielded good mummified plant fragments. Two new genera, *Trisacocladus* and *Apterocladus* are described and referred to the family Podocarpaceae. *Trisacocladus tigrensis* gen. et sp. nov. from Bajo Tigre is based on leafy shoots with male cones attached, as well as on female structures probably also connected organically to leafy branches. The male cones yielded 3-saccate pollen grains of the type usually referred to *Trisaccites*. *Apterocladus lanceolatus* gen. et sp. nov., from Bajo Grande, is also based on leafy shoots with attached male cones possessing pollen grains with three rudimentary air bladders. The following new species of fern-like cutinized fronds are described : *Pachypteris elegans*, *Almargemia incrassata* and *Ticoa lamellata* ; together with the conifers *Podocarpus dubius*, *Tomaxellia biforme*, and two new species of *Araucarites* (*A. minimus* and *A. baqueroensis*) both of which are based on ovuliferous scales.

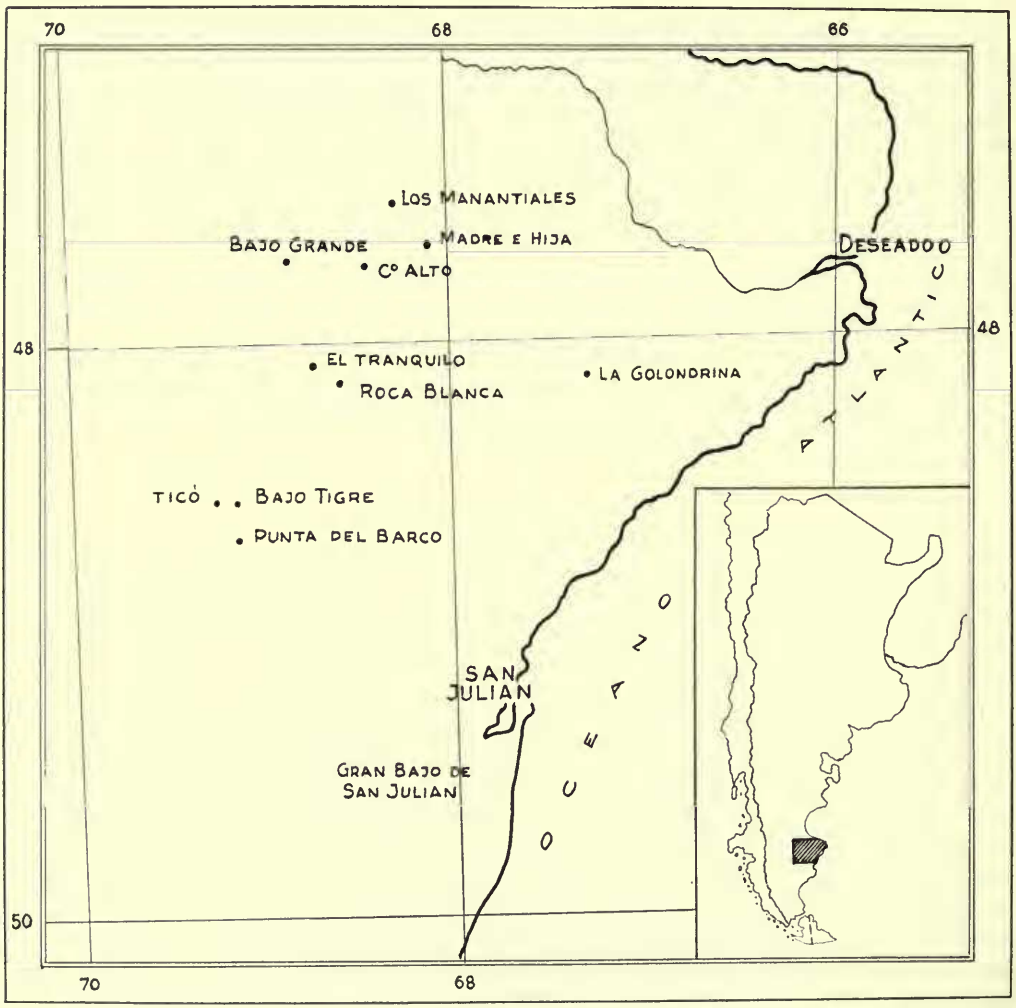
The original diagnosis of *Tomaxellia degiustoi* is revised in the light of new and better preserved material from the type localty (Ticó Amphitheatre). The description of these taxa adds considerably to the Lower Cretaceous flora of Patagonia which presently contains about 70 species, many with cuticular structure preserved.

I. INTRODUCTION

THE fossil plants described in the present paper were collected in the Ticó Amphitheatre, Bajo Tigre and Bajo Grande of Santa Cruz Province (Southern Argentina), during the years 1958–63. References to the Ticó and Bajo Tigre localities have already been made (Archangelsky 1963, 1965). The new locality, Bajo Grande, has been mentioned but without descriptions of its fossil plants.

The Baqueró Formation in Bajo Grande constitutes most of the " cliffs " (*barranca* in Spanish) which surround a large geographic depression (*bajo* in Spanish). In Bajo Grande, as in most localities, this formation is composed of nearly horizontal strata which cover sediments referred to the Matilde Formation of Middle to Upper Jurassic age. Bajo Grande is the third locality which has yielded mummified plant fragments ; the sediments being more indurated yielded a large variety of species. In Ticó and Bajo Tigre, the plants occur in lenticular beds at different levels in the sections. Each bed usually contains a few species only, but these are represented by many specimens, some of which are dominant in the association. The plants in Bajo Grande are usually more fragmentary and may have drifted for a longer distance before deposition. The only bed so far discovered in Bajo Grande has been named the *Araucarites* bed, because ovuliferous scales of this genus are very common, although other taxa are well represented.

The Baqueró Formation in Bajo Grande and elsewhere is divided into an upper and a lower member. The lower member, which includes the mummified plant material, has sediments of a somewhat darker colour and coarser grain (conglomerates, sandstones, etc. of grey, violet and similar colours) and is absent in some areas. The upper member is always white to yellow in colour and consists usually of volcanic ash (tuff). It is geographically widespread and may contain plant impressions or be totally devoid of fossils. The total thickness of the Baqueró Formation in all the areas so far surveyed, seldom exceeds 100 metres.



Map showing the main localities mentioned in the paper. In addition, the following three localities yielding rich floras are included : La Golondrina (Permian), El Tranquilo (Triassic) and Roca Blanca (Liassic).

On the evidence of the rich flora a Lower Cretaceous age is postulated for the Baqueró Formation, and all references to an Upper Cretaceous age should be abandoned. Consequently all correlations with the Upper Cretaceous Chubut Series (especially its Yellow Tuffs Formation or "*Tobas Amarillas*") are erroneous.

All previously recorded localities and those referred to in the present paper are represented in the map on p. 262.

The fossil plants described are all Gymnosperms. In 1965 references were made to a conifer associated with *Ginkgoites tigrensis*, having male and female cones in organic connection. This material, from Bajo Tigre, is here fully described and referred to the family Podocarpaceae. Good specimens of *Tomaxellia degiustoi* from the type locality in Ticó are also described and add to our knowledge of its gross morphology. The rest of the material described comes from the new Bajo Grande locality. Three species of cutinized fern-like fronds are referred to the genera *Pachypteris*, *Almargemia* and *Ticoa*. Two species of ovuliferous scales are included in the genus *Araucarites* (some material from Bajo Tigre and Ticó is also included in one of the species). Leafy branches with male cones in organic connection are referred to a new genus of the Podocarpaceae, *Apterocladus*, while sterile leafy branches are referred to a new species of *Podocarpus*. Finally a new species of *Tomaxellia* is described. The remaining material from Bajo Grande, which will be described in the near future, includes conifers of *Brachyphyllum* type, isolated male and female cones, Bennettitales and a few fern fragments.

The usual maceration technique (nitric acid followed by alkali) has been followed. Some delicate cuticles were treated only with very dilute alkali. A few transfers were also made.

The material studied belongs to the following collections: La Plata Natural History Museum (LP), Argentina; Lillo Institute of Tucuman (LIL), Argentina and the British Museum (Natural History) (BMNH, V.) Great Britain.

II. SYSTEMATIC DESCRIPTIONS

Gymnospermae

Abundant fern-like fronds possessing a thick cuticle are present in the Ticó flora. New generic names have been established for these based on cuticular characters (Archangelsky 1963); they were included in the Gymnosperms. The new material described here confirms the importance of these plants which occur in most of the localities where the Ticó flora has been found. In the absence of fructifications the natural relationship of these leaves is uncertain, but their cuticular structure strongly suggests their inclusion in the Pteridospermae and Cycadales. Three new species are described in the present work, *Ticoa lamellata* which resembles some living Cycads in epidermal characters, *Almargemia incrassata* also placed in or near the Cycads, and *Pachypteris elegans* which has characters in common with some Recent members of the Cycadales, although it also has similarities with the Pteridosperms. These leaves being abundant fossils must belong to species important in the Lower Cretaceous vegetation of Patagonia.

Genus *PACHYPTERIS* Brongniart 1828

Pachypteris elegans sp. n.

(Pl. 1, fig. 1 ; Pl. 2, figs. 10–12 ; Text-figs. 1–5)

Diagnosis. Leaf bipinnate, oblong, 5 cm. long × 2 cm. wide (base missing). Leaf rachis strong, 2 mm. wide. Pinnae opposite to subopposite, separated by 3–4 mm., lanceolate, up to 13 mm. long × 5 mm. wide, forming an angle of 45–60° with main rachis. Pinna rachis up to 1·5 mm. wide. Pinnules subopposite to alternate, arising at about 45° to pinna rachis, oblong to lanceolate with rounded apex and margins entire, up to 1·5 mm. long × 0·75 mm. wide ; lower margin decurrent and connecting with upper margin of pinnule below. Lower catadromic pinnule often once lobed and seated on the axil of pinna and main rachises. Mid-vein present up to near apex of pinnule, decurrent at base. Few simple lateral veins given off at acute angles. Substance of lamina thick.

Upper and lower cuticles up to 5 μ thick. Upper cuticle without stomata. Cells isodiametric, 25–50 μ, becoming rectangular near margins and on rachis. Anticlinal walls thick, unpitted, up to 5 μ, deeply cutinized. Cell surface finely granular. Lower cuticle with stomata ; shape and size of epidermal cells as for upper cuticle, except on veins which are marked by bands of rectangular cells in more or less longitudinal files. Trichome bases present on veins and rachises, sometimes between veins. Unicellular hairs have been observed.

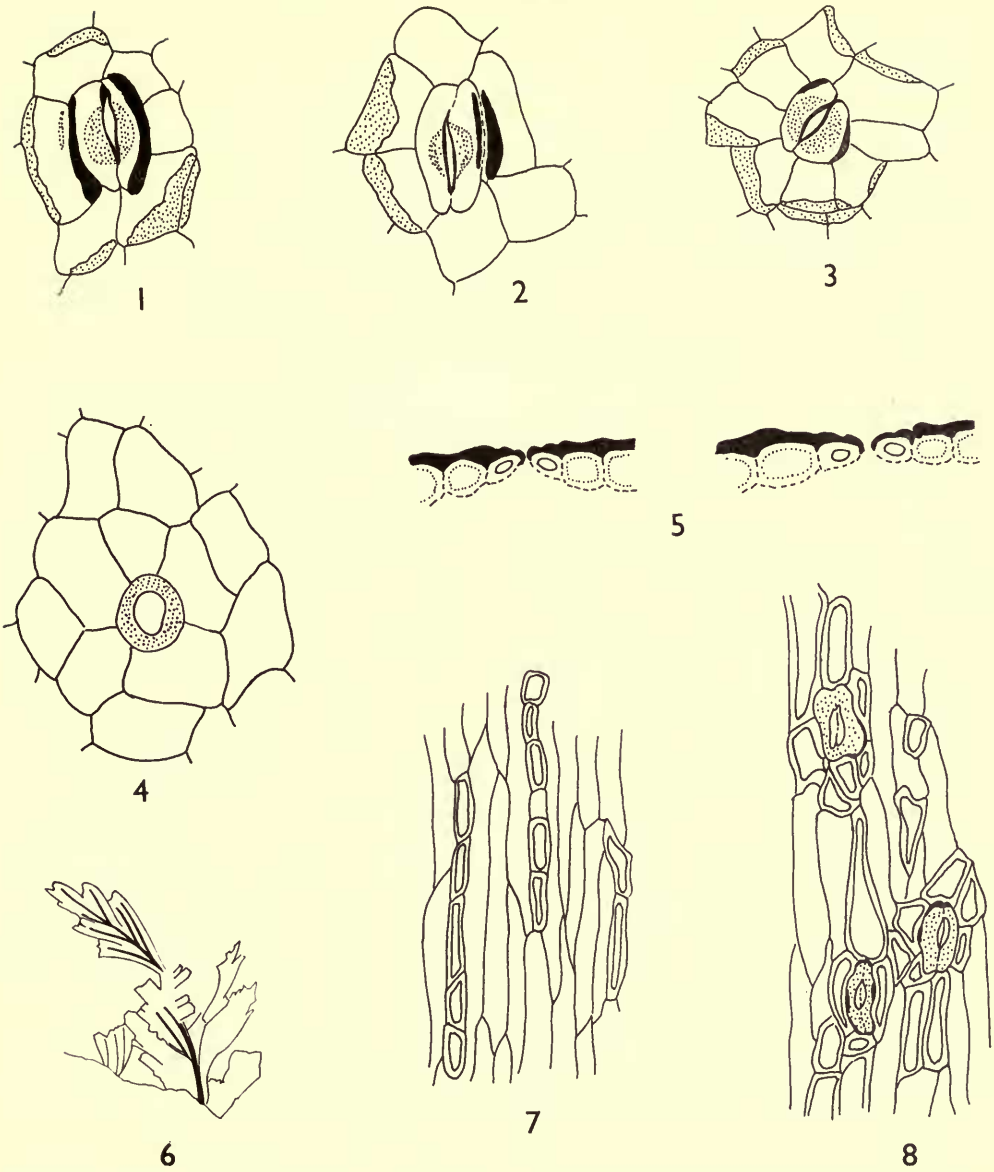
Stomata haplocheilic, densely disposed between veins on lower cuticle, typically monocyclic, sometimes imperfectly dicyclic, round or oval, having no definite orientation ; subsidiary cells often shared by two stomata. Guard cells little or not at all sunken. Subsidiary cells not much specialized, 6–7, not differentiated into polar and lateral, with cuticle considerably thickened on distal side (both periclinal and anticlinal walls). Guard cells cutinized, typically 40–50 μ long with dorsal and ventral walls sometimes thickened. A marked ring-shaped thickening surrounding aperture.

Holotype. LP 6233.

Material. In addition to the holotype, LP 6234–6249, BMNH, V.52266–75, LIL 2746–2752. Slides LP 167–173 ; BMNH, V.52276–78.

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed ; Estancia Bajo Grande, Santa Cruz Province, Argentina.

Description. *Pachypteris elegans* is a common element in the *Araucarites* bed of Bajo Grande. Its cuticle when macerated is yellow to pale brown in colour. The lower epidermis is readily distinguished by the presence of stomata which are completely absent on the upper cuticle. The guard cells are feebly cutinized and they present three pairs of rim-like thickened zones which surround the aperture. The inner, near the aperture (ventral) is the less marked. The outer thickening (dorsal), near the contact with subsidiary cell is well marked. Finally a median thickening between the inner and outer is sometimes developed and may be fused with the inner one. When present, it may be finely granular.



FIGS. 1–5. *Pachypteris elegans* sp. n. Figs. 1–3, Stomata showing strong cutin thickenings (black) and less marked ridges (dotted) on guard cells and on subsidiary cells. Slide LP 169, ×370. Fig. 4, Hair base. Slide LP 169, ×370. Fig. 5, Section of stomata, ×370.

FIGS. 6–8. *Almargemia incrassata* sp. n. Fig. 6. Outline of holotype. LP 6255, ×1. Fig. 7. Portion of upper epidermis showing two types of cells. Slide LP 184, ×180. Fig. 8. Portion of lower epidermis showing stomata and two types of epidermal cells. Slide LP 184, ×180.

The stomatal aperture is slightly sunken, the poles of the guard cells being somewhat raised.

Stomata with only two large subsidiary cells have been seen.

Discussion. Harris (1964) emended the original diagnosis of *Pachypteris* (and included the genus *Pachydermophyllum* Thomas & Bose in it). This new diagnosis is based on general morphology of the frond as well as on its cuticular structure. The present species is included in *Pachypteris* because there is agreement in the shape of the fronds and their pinnules as well as in venation. There are, however, some differences in the cuticle : (a) the stomata are restricted to the lower epidermis in *P. elegans*, while those of the European species are amphistomatic (although very few stomata occur on the upper epidermis) ; (b) the guard cells of stomata are not much sunken in *P. elegans* and have thickened dorsal and ventral walls, plus the ring-shaped structure round the aperture. These differences characterize the new species, the third one with cuticle preserved (the other two being *P. lanceolata* and *P. papillosa*).

Among similar fern-like fronds from the Ticó flora, *Mesosingeria* although having comparable pinnules, differs in the lack of a definite mid-vein and in its cuticular structure, especially the stomata which are deeply sunken with a protective tube of cutine projecting outwards. *Ticoa* differs mainly in its stomatal apparatus (usually with a large epistomatal chamber) and in the shape of its epidermal cells which are normally elongated and not isodiametric. Moreover, the basal catadromic pinnules are never decurrent on the pinna rachis. The stomatal apparatus of *Mesodescolea* has in common the thickening of the guard cells on the dorsal walls as well as the median ring-like thickening, which is more pronounced. Ventral walls of subsidiary cells of this genus may also be thickened. In its gross morphology, the leaf of *P. elegans* is three times pinnate and has a fern-like appearance, while *Mesodescolea* is twice pinnate and has a wide pinnular lamina. There are some differences in cuticular structure. *Ruflorinia* also has guard cells with a median thickening round the aperture, but the shape of the guard cells is oval, corresponding to the shape of the stomatal apparatus. The lips of the guard cells are also different (strongly thickened) while no dorsal thickenings occur on these cells. The distribution of stomata and the number of subsidiary cells is markedly different.

Some species of the form genus *Scleropteris* (e.g. *S. pomelii* Sap.) may be compared with *P. elegans*, but as there is no information about the cuticle further comparisons are not possible. *Scleropteris* is a highly unnatural assemblage of species, probably uniting taxa of different natural orders (Archangelsky 1963*a*).

The peculiar thickenings on the guard cells of *P. elegans* are comparable with those found in the living Cycadales *Stangeria paradoxa* and *Bowenia spectabilis*. The stomata of both living genera have, like *P. elegans*, little or not at all sunken guard cells. The ventral walls of the guard cells are cutinized in all three taxa. *Stangeria* and *P. elegans* have dorsal walls of subsidiary cells with cutinized ridges (sometimes in the fossil species there are two parallel ridges of cuticle, one on the guard cell and the other on the limit of guard and subsidiary cell). The median ring-like thickenings on the guard cells are absent in *Stangeria* but may be seen in *Bowenia*. In all three

taxa the stomata are monocyclic to imperfectly dicyclic. The external morphology of the leaves in *Stangeria* and *Bowenia* differs considerably from the fronds of *Pachypteris elegans*.

This Patagonian fossil may well be one of the latest representatives in Southern floras of that imperfectly known group of " Mesozoic Pteridosperms ", which on the one hand has some similarities with the true Cycadales while on the other has characters of its own. The fructification *Pteroma* (Harris 1964) which is supposed to be the microsporophyll of *Pachypteris papillosa*, may throw some light on the true relationships of this group.

Genus *ALMARGEMIA* Florin 1933

Almargemia incrassata sp. n.

(Pl. 1, figs. 3, 4 ; Pl. 3, figs. 13, 14 ; Text-figs. 6–10, 13)

Diagnosis. Leaf (fragmentary) simply pinnate. Rachis delicate, 1·5 mm. wide. Pinnae subopposite, inserted at angle of about 45° (more acute towards apex), with decurrent catadromic side and constricted anadromic side, oblong, with broadly dentate apex, up to 1 cm. long × 0·4 cm. wide at the middle ; lateral margins dentate towards apical sector. Uniform veins, 3–4 per pinna, parallel to margins, converging at base. Fine lines between veins clearly differentiated.

Both cuticles 2 μ thick, with markedly elongated and similar epidermal cells, about 20 μ wide. They are of two kinds : (1) numerous, with thin anticlinal walls (1 μ) and (2) less numerous, with thick anticlinal walls (7 μ), and less elongated. The thick-walled cells form longitudinal rows one, or occasionally more than one, cell broad. Cells on rachises markedly elongated with the same two types of thin and thick-walled cells and occasional papillae on the thick-walled cells.

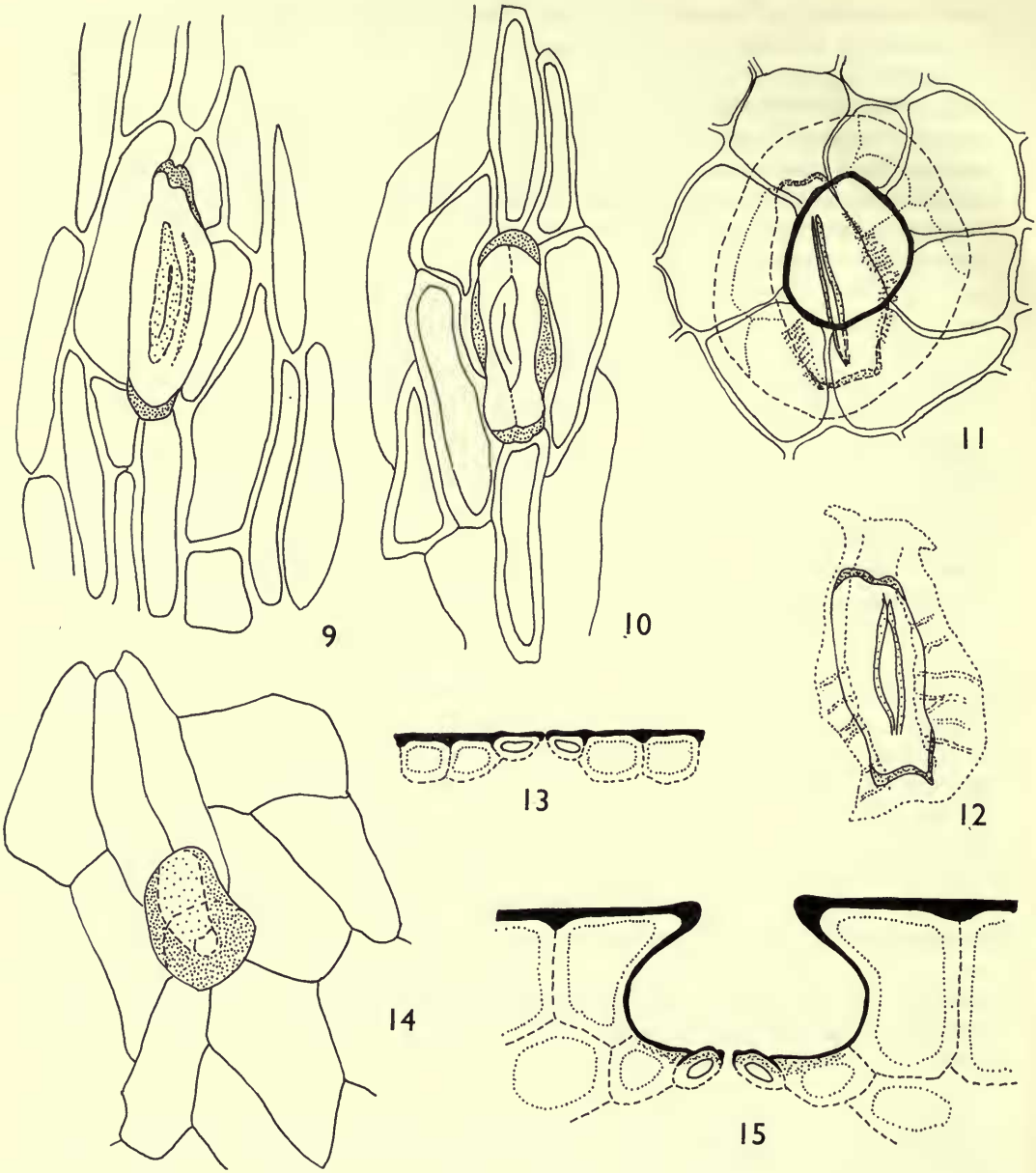
Stomata present on lower cuticle only, longitudinally orientated, sometimes obliquely, placed in rows of thick-walled cells, typically monocyclic to imperfectly dicyclic. Subsidiary cells typically 4–6 in number. Polar subsidiary cells occasionally differentiated ; longer than lateral subsidiary cells which sometimes slightly overhang guard cells. All subsidiary cells usually thick-walled (there are a few exceptions). Stomata sometimes with subsidiary cells in contact. Guard cells with poles on epidermal surface and aperture slightly sunken, 50–55 μ long. Poles, ventral and dorsal walls strongly cutinized. Longitudinal ridge of cutin occasionally present near dorsal wall of guard cells.

Holotype. LP 6255.

Material. In addition to the holotype, LP 6254 ; BMNH, V.52264. Slides. LP 184 ; BMNH, V.52265.

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed ; Estancia Bajo Tigre, Santa Cruz Province, Argentina.

Description. *Almargemia incrassata* sp. n. is represented by only two fragmentary specimens. LP 6254 is a leaf fragment about 3 cm. long. It shows a few pinnae on both sides of a slender rachis. The pinnae are poorly preserved but show the



FIGS. 9, 10, 13. *Almargemia incrassata* sp. n. Figs. 9, 10. Stomata. Slide LP 184, ×500. Fig. 13. Section of stoma, ×500.

FIGS. 11, 12, 14, 15. *Ticoa lamellata* sp. n. Fig. 11. Stoma showing sunken guard cells, large pit and remnants of lamellae. Slide BMNH. no. V.52263, ×500. Fig. 12. Guard cells of a stoma showing remnants of lamellae. Slide LP 174, ×500. Fig. 14. A trichome. Slide BMNH. no. V.52263, ×500. Fig. 15. Section of stoma, ×500.

main morphological characters. The cuticle is well preserved and is resistant to maceration, after which it remains as an almost colourless film. The other leaf fragment (LP 6255) bears three complete pinnae, clearly showing the shape with its characteristic dentate margins. The fine lines between veins mentioned in the diagnosis clearly correspond to rows of thick-walled epidermal cells. This character of thick and thin walled cells on the same epidermis is known to occur among Recent Cycadales and has been fully discussed by Pant & Nautiyal (1963). The stomata are typically exposed with their poles of guard cells curved towards the surface, while the aperture is slightly sunken. This character, which is also common to both living and fossil Cycadales, is also found in the genus *Ticoa* although not so sharply marked as in *Almargemia*. The ventral and dorsal thickenings of the guard cells are conspicuous ; the contact area between guard and subsidiary cells (dorsal wall of guard cells) is also thickened, usually a little less than the other thickenings mentioned. In a few cases, guard cells with strong dorsal ridges parallel to the dorsal walls of the guard cells were observed. Also the subsidiary cells may slightly overhang the guard cells. All these characters related to the thickenings of the guard cells are found in most of the living Cycadales. Thus *Almargemia incrassata* is another element of the Ticó flora which may be placed in or near the Cycadales, in its strict sense, and agrees with Florin's (1933) observations on the type species of the genus, *A. dentata* (Heer) Florin.

Discussion. Among fossil leaves with a similar pinnate plan, *A. incrassata* is most similar to the type species of the genus, *A. dentata* (Florin 1933 : 100). Leaves of the European species are pinnate with dentate margins, and are borne on slender rachises with a similar plan of venation. Differences in morphology are of specific significance : the size of the pinnules and the number of veins is greater in *A. dentata*, while in *A. incrassata* the margins of pinnae are more dentate. The cuticles agree in having epidermal cells of two sorts, but in *A. incrassata* thick walled cells form definite longitudinal rows while in *A. dentata* they are usually isolated or occur in small groups. Stomata of both species are typically surrounded by thick-walled cells with 4–6 subsidiary cells. The guard cells are alike in both species.

Teixeira (1948) figures *A. dentata* from Almargem (pl. 18, figs. 9–11) and from Belas (pl. 21, figs. 4–7), but adds no diagnostic characters to the original description. In these specimens, the shape of the pinnules is clearly different from *A. incrassata*. *A. dentata* is recorded from the Lower Cretaceous (Aptian) of Portugal. Thus the geographic distribution of the genus and probably its geological range are extended.

Genus ***TICOA*** Archangelsky 1963

Ticoa lamellata sp. n.

(Pl. 1, figs. 2, 8, 9 ; Pl. 3, figs. 15, 16 ; Text-figs. 11, 12, 14, 15)

Diagnosis. Leaf at least bipinnate. Segments incomplete, at least 3 cm. wide with rachis 2 mm. wide. Pinnae lanceolate up to 1·4 cm. long × 0·5 cm. wide, ending with acute pinnule, inserted at an angle of about 75°, alternate, slightly

overlapping adjacent pinnae. Pinnules alternate, inserted at an angle of about 70°, up to 4 mm. long × 1·5 mm. wide, slightly decurrent, lanceolate, constricted at base. Those towards proximal part of pinnae (near rachis) more oblong, with rounded apex and margins entire (not lobed). Veins not seen.

Both cuticles of similar thickness, 3 μ. Upper cuticle having no stomata but numerous trichomes. Cells markedly elongated, parallel to margins, with straight walls. Cells of lower cuticle elongated near margins and on veins, somewhat isodiametric or wedge-shaped near stomata and trichomes, slightly elongated on rest of lamina. Cell surface flat ; anticlinal walls straight, sometimes pitted. Cells on rachises markedly elongated ; trichomes and elongated stomata present. Anticlinal walls thicker than those of lamina.

Stomata usually dicyclic, avoiding veins and margins, longitudinally orientated, parallel to veins and margins, 25–40 per sq. mm. Guard cells strongly sunken in round or oval pit, formed by subsidiary and encircling cells. Encircling cells typically 6–8, forming sides of pit, about 40–50 μ wide. Mouth of pit typically 40–50 μ wide, situated at the same level as epidermis or slightly raised. Subsidiary cells small, at bottom of pit ; guard cells 50–60 μ long, well cutinized, with cutin thickenings on dorsal and ventral walls. Poles of guard cells raised and strongly cutinized. Transverse striations occur on dorsal walls of guard cells, extending on both sides. They may belong to the remnants of lamellae.

Trichomes single, sometimes in pairs, composed of an isodiametric cell, 25–35 μ in diameter, with thick anticlinal walls, about 7–9 μ. Free part composed of single cutinized hair with thick lateral walls.

Holotype. LP 6250.

Material. In addition to the holotype, LP 6245*b* ; BMNH, V.52262. Slides LP 174 ; BMNH, V.52263.

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed ; Estancia Bajo Grande, Santa Cruz Province, Argentina.

Description. The material consists of fragmentary specimens preserved as black compressions on a pale grey matrix. When macerated the cuticle appears as a pale yellow film and is quite resistant to chemical treatment. The impressions of the pinnules show no traces of veins. However, on the lower cuticle a median longitudinal strip devoid of stomata may well represent the mid-vein. Lateral veinlets were not observed.

Discussion. This species is closely comparable with *Ticoa harrisii* in the size of pinnules. However *T. lamellata* has pinnae and pinnules inserted at a wider angle (70–75° against 45° in *T. harrisii*). Pinnules of the new species are usually constricted at the base ; no lobation of basal pinnules was seen. The cuticle is of the same thickness on lower and upper epidermis while in *T. harrisii* the upper cuticle is thicker than the lower. The stomatal number is slightly higher in *T. lamellata* while the number of encircling cells is lower (6–8 against 8–10 in *T. harrisii*). Hair bases in *T. lamellata* do not show inwardly cutinized extensions as seen in *T. harrisii* and *T. magnipinnulata*. Finally, the guard cells in *T. lamellata* have their poles more

strongly cutinized; also, the probable remnants of lamellae while constant in the new species, were not observed in the others. *T. magnipinnulata* on the other hand, differs in the size and shape of pinnules as well as in stomatal structure (it has 3 cycles of cells forming the stomatal pit).

Ticoa is another leaf genus whose leaves may be compared with those of other genera so far as their shape is concerned. All three species are alike in cuticular and especially in stomatal structure. The shape and size of leaves, however, are more varied, *T. harrisii* and *T. lamellata* being closer to each other than to *T. magnipinnulata*. The two former species may be compared with *Pachypteris* only in the shape of pinnules, although the lamina of basal pinnules does not extend to the segment rachis. The cuticles of the two genera differ in the shape of their epidermal cells and in stomatal structure. Trichome bases with cutinized anticlinal walls are constantly present in *Ticoa* but absent in other similar leaf genera.

Coniferales

The six species of conifers so far known in the Ticó flora have been referred to the genera *Brachyphyllum*, *Athrotaxis* and *Tomaxellia*. Most of them are numerically important in the different beds of the Ticó Amphitheatre. Other conifers were subsequently found in Bajo Tigre and Bajo Grande, and some of them will be described here. Isolated ovuliferous scales are referred to the Araucariaceae, confirming the presence of this family in the Ticó flora. The Podocarpaceae are represented by several species, some with male and female structures. The suspected presence of this family (Archangelsky 1963) is therefore also confirmed. A new species of *Tomaxellia* is also described.

The Podocarpaceae and the Araucariaceae appear to be the best represented families of conifers in the Lower Cretaceous of Patagonia. They are represented by numerous species each with a large number of individuals. Many other conifers have been collected from different localities of the Ticó flora (some of them probably belonging to these families). The pollen content of some beds shows a high number of bisaccate pollen grains (as well as trisaccate) which may well have been derived from species of the Podocarpaceae.

Family **ARAUCARIACEAE**

Genus ***ARAUCARITES*** Presl 1838

The generic name *Araucarites* is used for cones, isolated ovuliferous scales and sterile twigs having " araucarian affinity " (Seward 1919 : 256). While it is possible to relate female structures with some security to the living Araucariaceae, the assignation of sterile twigs is less secure even when the cuticular structure is preserved.

The two species described here are isolated ovuliferous scales showing a single median embedded ovule and a ligule supported by wide lignified bracts.

Araucarites baqueroensis sp. n.

(Pl. 1, fig. 5 ; Text-fig. 17)

1951 *Araucaria* (section *Colymbea*), Feruglio : 65.

Diagnosis. Cuneiform ovuliferous scale with lateral wings and acuminate apex about 3 mm. long. Width of scale 2 cm., length 2–3 cm. A single oval seed immersed in the scale is typically 1–1·5 cm. long × 4–5 mm. wide, broadest near distal end. Delicate wings expanded laterally up to 0·8 cm. from edge of seed. Ligule short, not exceeding external margin of bract, maximum width about 1 cm.

Holotype. LP 5766*b*. (Cerro Testigo bed.)

Material. In addition to the holotype, LP 5767*b*, 5768*b*, 5770 (Cerro Testigo bed) ; LP 6345–46 ; BMNH, V.52254 (*Araucarites* bed) ; LP 5277*b* (*Cladophlebis tripinnata* bed) ; LP 5369*c* (*Ticoa harrisii* bed).

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member. Estancia Bajo Tigre (Cerro Testigo bed) ; Estancia Bajo Grande (*Araucarites* bed) and Ticó Amphitheatre (*Cladophlebis tripinnata* and *Ticoa harrisii* beds), Santa Cruz Province, Argentine.

Description. *Araucarites baqueroensis* is based on numerous ovuliferous scales from different localities, those from the Cerro Testigo bed in Bajo Tigre yielding the most abundant and best preserved. They are usually fragmentary and are associated with abundant broad twigs referred to *Brachyphyllum*. Only impressions were found in this bed which consists of a fine-grained, pale brown sediment, similar to the Ticó or other Bajo Tigre horizons bearing mummified plant fragments. However, in this bed oxidation has destroyed all cuticles.

The scales are large, much larger than those of the other species, *A. minimus* from Bajo Grande. In *A. baqueroensis* the ligule is well defined, being separated laterally from the wing of the bract by a visible ridge (which is a mould of the cavity left in the original compression, between the tissue of the bract and the ligule). Near the apex, the ligule is broader but does not exceed the length of the bract. The field between the external distal margin of the bract and the seed is large, more than 5 mm. long. Most specimens are broken ; seeds or seed ligules are commonly found isolated from the bract, but a few specimens show clearly the seed ligule and their bracts which have wing-like lateral expansions. The acuminate apex is usually broken but can be seen in some specimens projecting for a short distance. Two fragmentary remains of what I believe to be the same species were found in Bajo Grande. One of them (LP 6346) shows a distinct acuminate apex of the bract projecting for 3 mm., distally broken. The specimen from the *Cladophlebis tripinnata* bed in Ticó is also fragmentary but agrees with the typical material. The one from the *Ticoa harrisii* bed is slightly larger (about 3 cm. long, incomplete), and shows the characters of the species.

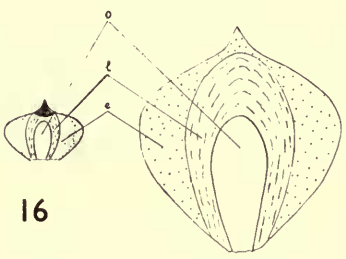
Discussion. *Araucarites baqueroensis* differs in size and shape from the other species (*A. minimus*) described in the present paper.

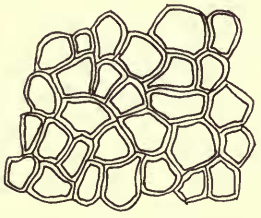
Araucaria sp. as described by Berry (1924) from the Jurassic of Santa Cruz

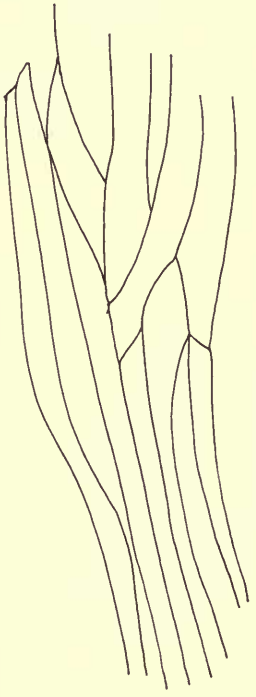
Province (Argentina) is similar in size and general shape, but the ligule appears much narrower than in the present species, especially in its distal sector.

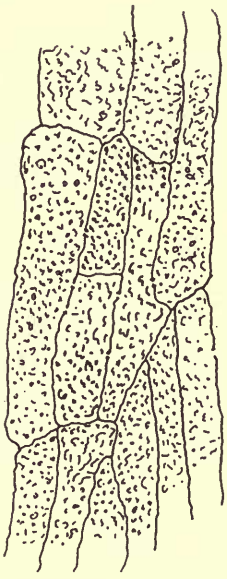
Feruglio's *Araucaria* sp. from Cerro Cuadrado and Punta del Barco may well belong to *Araucarites baqueroensis*, but only a brief description and no figures are available. It was found in the same formation but in the upper member where the plant association is somewhat different.

Some specimens from Graham Land described as *Araucarites cutchensis* Feistm. by Halle (1913*a*, pl. 8, figs. 5, 7, 8) are similar in size and shape but they have a pointed acuminate apex and a narrower ligule. The type specimens described by Feistmantel (1876) are also similar to *A. baqueroensis* but they show a long acuminate apex (Feistmantel 1876, pl. 9, fig. 1), although this is lacking in some of the specimens. In subsequent publications, the same author included markedly different forms in this species (cf. Feistmantel 1877, pl. 14, figs. 6, 8).









FIGS. 16, 18–20. *Araucarites minimus* sp. n. Fig. 16. Ovuliferous scale (reconstructed), ×1. *o*, ovule; *l*, ligule; *e*, bract. Fig. 18. Cells of outer membrane. Slide LP 233, ×370. Fig. 19. Cells with straight and unpitted walls of membrane (3) of diagnosis. Slide LP 235, ×370. Fig. 20. Cells of granulose membrane (2) of diagnosis. Slide LP 234, ×370.

FIG. 17. *Araucarites baqueroensis* sp. n. Ovuliferous scale (reconstructed), ×1. Lettering as for Fig. 16.

Araucarites minimus sp. n.

(Pl. 1, figs. 6, 7 ; Text-figs. 16, 18–20)

Diagnosis. Broadly cuneiform ovuliferous scales with well developed lateral wings and acuminate apex up to 3 mm. long. Width of scale typically 8 mm. length at least 7 mm. broken at base of attachment. Single oval seed immersed in scale, typically 3·5–5 mm. long × 2–2·5 mm. wide, broadest near distal end. Delicate wings expanded laterally up to 3·5 mm. from edge of seed, with irregularly lobed margins, showing sinuous bands of probably fibrous cells. Short ligule, not exceeding external margin of bract, about 3–4 mm. wide, sometimes seen.

Four cutinized membranes present : (1) Outside of scale, including outside of integument of seed, rather strong, finely granular with more or less isodiametric cells, about 20–30 μ in diameter, usually with rounded contours and thick anticlinal walls (up to 4 μ). Membrane on wings becoming very delicate and losing all traces of cell contours. Dark contents usually adhering to this membrane, forming definite bands disposed in close files. (2) Thin granular membrane showing markedly elongated cells, 15–20 μ wide, with anticlinal pitted and minutely crenulate walls. (3) Thin membrane with markedly elongated cells, 5–15 μ wide, but showing no granules on surface, with straight, unpitted walls. (4) Structureless strong membrane, probably corresponding to megaspore wall.

Holotype. LP 6329.

Material. In addition to the holotype, LP 6328, 6330–44 ; LIL 2739–2745 ; BMNH, V.52255–60. Slides LP 231–235 ; BMNH, V.52261.

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed ; Estancia Bajo Grande, Santa Cruz Province, Argentina.

Description. *Araucarites minimus* is abundant in Bajo Grande. The delicate wings may be lacking, but this is probably an accident of preservation. The size of the seed is fairly uniform. The seed is embedded in the scale and covered by its surface. It occupies a hollow cavity which may be filled with mineral substances (powdery calcite or limonite) or preserved as a carbonized body. These coal fragments when treated with dilute alkali show three types of membranes (membranes 2–4 of the diagnosis). The two membranes with narrow and elongated cells might both belong to the nucellus cuticle but I prefer merely to designate them as membranes 2 and 3 until more material shows their true nature. The rest of the scale is also covered by a carbonaceous film which is broken into small fragments. These fragments after treatment with dilute alkali, show the same type of membrane, assumed to be the outside of the scale. It is similar on the acuminate apical sector, on the base and top of the seed. The ligule is usually broken, but in a few specimens it is seen to be similar to that of *Araucarites phillipsii* described by Kendall (1949 : 155, text-fig. 1B).

Discussion. I have referred these scales to the Araucariaceae because they have one seed and the remnants of a ligule embedded in the bract. The size of the scales makes it possible to estimate the approximate size of the female cone, which might

have been about 2 cm. in diameter (relatively small for the Araucariaceae). Most of the living species have large cones and so has the fossil *Araucaria mirabilis* (Spegazzini) described and figured by Calder (1953) from the Jurassic of Santa Cruz Province. Furthermore, it is possible to include *A. minimus* in the *Eutacta* section of the genus *Araucaria*, because the scales of the other two sections, viz. *Bunya* and *Colymbea* are of a different type. As already pointed out by Berry (1924) and others, it is curious that the two living representatives of the family in South America, *Araucaria araucana* (Mol.) K. Koch and *A. angustifolia* (Bertolini) O. Kuntze, belong to the *Colymbea* section, while all fossil representatives so far found in the same area may be classed in the *Eutacta* section, including the two species from Ticó.

Fossil material referred to *Araucarites* (cone scales) has been described from Jurassic and Lower Cretaceous strata in South America. Halle (1913*a*) describes several female cone scales from the Middle Jurassic of Graham Land. All this material is included in Feistmantel's *Araucarites cutchensis* described from the Jurassic of India which represents a rather unnatural assemblage. All the figured specimens (Halle 1913*a*, pl. 8, figs. 3–8) are much larger than ours and have a longer acuminate apex. The original description of *A. cutchensis* is poor, but judging from Feistmantel's (1876) figures *A. minimus* differs in shape and is much smaller. The specimens of *A. cutchensis* figured by Feistmantel (1877) are also different in size and shape. There are also differences in the shape of the scales figured by Feistmantel (1879), although they are closer in size to *A. minimus*. *Araucarites macropterus* Feistmantel is much larger than *A. minimus*.

Berry (1924) described cone scales of *Araucaria* sp. from the Laguna del Carbón, in the Gran Bajo de San Julián, Santa Cruz Province.[1] These scales differ in shape and size from *A. minimus* by having a less developed wing and a shortly acuminate apex. Feruglio (1951) described scales of *Araucaria* from the Laguna del Molino of the Gran Bajo de San Julián, Santa Cruz, which he considered as Upper Jurassic or Lower Cretaceous. No figures were given, but the description suggests that they are larger. In the same paper, Feruglio briefly described other scales from the Punta del Barco and Cerro Cuadrado localities, comparing his material with that described by Berry (1924), and therefore different from ours.

Araucarites nipaniensis Singh (1957) from the Jurassic of India, although only slightly larger than *A. minimus* differs in the shape of the seed and in having a large distal field between seed and margin of bract. No acuminate apex has been reported in this species.

Araucarites phillipsi Carruthers from the Jurassic of Yorkshire, as described by Kendall (1949) is larger (up to 1·7 cm. long). It agrees in having a short ligule but the acuminate apex of the bract is not as prominent as in our species. The wings

[1] I have doubts as to the age of these sediments which Berry described as Rhaetic. Feruglio (1951) considers that the Gran Bajo de San Julián strata which contain these plants are either Jurassic or Lower Cretaceous. Stipanicic (1957) in a complete geological survey of this area, concludes that the Laguna del Carbón section (as well as all other similar exposures in the Gran Bajo de San Julián) belong to his Matilde Formation, Middle to Upper Jurassic in age. The facts given to ascertain this age are not conclusive ; there are few plants, most of them useless for precise age determination, such as *Cladophlebis*, *Sphenopteris*, *Ptilophyllum* and *Podocarpus*. The mention of *Athrotaxis* cf. *ungeri* points to a relation with the Baqueró Formation or similar strata from the Lago San Martin area, also in Santa Cruz Province.

in *A. minimus* are also more developed. The epidermis of the cone scale differs in its more elongated cells but the cells of the nucellus cuticle are similar and so is the megaspore membrane.

Family **PODOCARPACEAE**

Genus ***TRISACOCLADUS*** nov.

Derivation of name. *Trisaco*, three air bladders of the pollen grains, *cladus*, leaf.

Diagnosis. As for the only species, *Trisacocladus tigrensis* sp. n.

Trisacocladus tigrensis sp. n.

(Pl. 4, fig. 21 ; Pl. 5, figs. 22–39 ; Pl. 8, figs. 56–67 ; Text-figs. 21–25)

Diagnosis. Twigs branched, widest seen 0·6 cm. and longest 5 cm. (base and apex broken). Leaves disposed in a close spiral, when detached from branch leaving a marked rhomboidal cushion with a slight depression, probably representing the vascular supply. Leaves radially disposed or spreading in one plane, with rounded apex, decurrent, with margins entire, typically 5–6 mm. long × 0·8 mm. wide. A median longitudinal depression suggesting the mid-vein sometimes seen. Substance of lamina thick.

Male cones axillary, attached and shortly pedunculate, oval, gradually tapering towards apex, smallest seen 9 mm. × 3 mm., largest 15 mm. × 4·5 mm. Central axis straight, up to 2 mm. wide. Microsporophylls spirally arranged, inserted at right angles to axis (sometimes more than 90°) composed of a main branch expanding at distal end into a head also placed at right angles (parallel to cone axis). Head extending upwards as short laminar projection, up to 3 mm. long, covering base of next sporophyll. Head also extending downwards as short keel. Two (or more?) oval pollen sacs present, up to 1 mm. long. Cuticle of sporophyll delicate, showing more or less elongated cells, 10–15 μ wide, with straight walls. Membrane of pollen sac appearing structureless and irregularly granulose. Pollen usually of *Trisaccites* type, varying in shape and size from 12–32 μ in equatorial diameter. Equatorial outline somewhat triangular, sometimes round or oval. Three (sometimes two) small air bladders usually present on distal half of body. Exine of body appearing psilate or faintly foveolate, while on wings it may be reticulate. Margins of air bladders finely crenulate.

Female cone-like structures probably laterally inserted on branches, subtended by a few sterile leaves. Longest cone seen 2 cm. × 7 mm. wide. Central fleshy axis, 2–6 mm. wide, bearing irregularly (or bilaterally?) erect ovules (and small linear bracts up to 5 mm. long?). Ovules orthotropous, close together, typically oval, 2–3 mm. long × 1·5–2 mm. wide composed of three cutinized layers : (1) innermost delicate membrane, finely granular, showing no structure, assumed to be the megaspore wall ; (2) thin membrane showing elongated narrow cells, 5–15 μ wide, projecting into short acuminate apex ; cells becoming much shortened towards base and apex, assumed to be the nucellus ; (3) outer membrane showing no structure but

many circular granules irregularly disposed or tending to form ill-defined files assumed to be the integument. Impressions of ovules show longitudinally elongated bulging meshes crowded with small circular granules, tending to be disposed in files.

Seeds developing a stone, showing a marked micropilar projection and meshes on outer surface, crowded with small granules.

HOLOTYPE. LP 5826 (*Trisacocladus* bed).

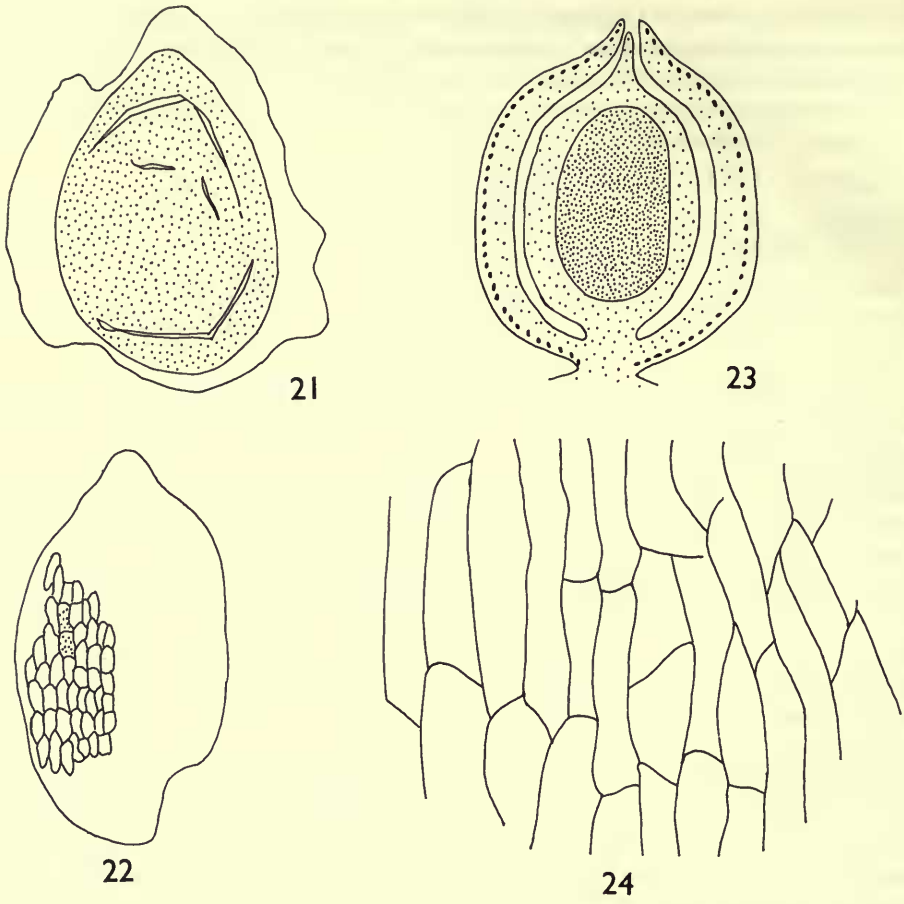
MATERIAL. In addition to the holotype LP 5827–42, 5844–50, 6157–69, 6175–81, 6211–32; BMNH, V.52235–38, V.52240–50, V.52252–53 (*Trisacocladus* bed); LP 6182–91 (*Ginkgoites tigrensis* bed); LP 5818*b*, 6170–74, 6430–39; BMNH, V.52239, V.52251 (Upper bed). Slides LP 54–65, 155–166, 244, 300–302; BMNH, V.52234.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Trisacocladus*, *Ginkgoites tigrensis* and Upper beds. Estancia Bajo Tigre, Santa Cruz Province, Argentina.

DESCRIPTION. This plant occurs in a newly discovered bed of the Bajo Tigre here referred to as the *Trisacocladus* bed. Deep horizontal tunnels made by coal miners enabled me to collect abundant material. The bed extends horizontally and is located on the roof of these tunnels. It yielded abundant *Trisacocladus tigrensis* branches and cones and also freshwater phyllopods but no other fossils. The rock is pale brown in colour and the fossils are dark brown. The matrix is fine grained, but a few centimetres below this layer the grain becomes coarser and the rock includes many coal fragments, some of considerable size.

Numerous branches have radially disposed leaves but one specimen shows leaves spreading in one plane. Both types are here considered as belonging to the same plant. No trace of cuticle was found. All attempts, including transfers, failed. The leaves are usually covered by a very fragile film which may be the mineralized remnant of the cuticle, but it shows no structure. The phyllotaxis of the leaves is probably 3/8. Fragments of this conifer were also found in other beds of Bajo Tigre (*Ginkgoites tigrensis* and Upper beds, about 5 metres above).

The holotype shows clearly the attachment of a male cone to a short fragmentary branch. On the axis of this attachment a few linear leaves up to 6 mm. long are present, and they are comparable to those found on the sterile branches. All the other male cones were found isolated. As their shape, size and pollen content are very similar to the holotype, they are all placed in *Trisacocladus tigrensis*. It is not clear whether the pollen sacs are placed on the adaxial or abaxial surface of the sporophyll, but as they are believed to be of podocarpaceous affinity, I presume their position is abaxial. Many cones have their pollen sacs still preserved as coaly oval bodies which may be easily separated and treated with very dilute alkali. In such sacs the pollen is also well preserved. Similar cones yielding pollen grains of the same type are also found in the *Ginkgoites tigrensis* bed associated with comparable sterile twigs. One of these cones (LP 6184) has at its base a few leaves similar to those described for the holotype. In the Upper bed, *Ginkgoites* is missing while *Trisacocladus* becomes abundant. Many twigs and male cones are found in associa-



FIGS. 21–24. *Trisacocladus tigrensis* gen. et sp. n. Fig. 21. Two membranes seen on a translucent specimen. Inner (dotted) belongs to the megaspore membrane; the outer is the nucellus membrane. Slide LP 159, ×25. Fig. 22. Outlines of the elongated bulging meshes (two with crowded small granules) seen in impressions of seeds. LP 5849, ×25. Fig. 23. Ideal section of the ovule showing megaspore membrane, nucellus and integument (with inner content). ×25. Fig 24. Cells of cuticle of the microsporophyll. Slide LP 50, ×370.

tion. The pollen grains and the gross morphology of twigs and leaves are in all respects similar.

When preparing the pollen sacs, many grains were found still attached to the irregularly granulose membrane, although most of them spread free when the sac burst. The three small air bladders give the grains a typical appearance, similar to the sporomorphs described as *Trisaccites* from Australia, Tasmania and New Zealand (Cookson & Pike 1954, Couper 1960). In the present material the bladders are flattened in the distal half of the body (unexpanded). However, in the same

pollen sacs a few grains with turgid bladders have been found. Such grains closely resemble the sporomorph *Microcachrydites*, found also in Australia, New Zealand, Tasmania and Antarctica. A detailed study of the pollen grains from Bajo Tigre has been published by Gamerro (1965).

Only one specimen (LP 5846) shows what may be an organic attachment of a female cone to a shoot bearing *Trisacocladus tigrensis* leaves. A few leaves are placed in the axil of the shoot and the presumed base of the cone.

The typical fleshy axis of the cone is conspicuous and shows many adhesions, mainly quartz grains and *Triletes* type megaspores; it was probably sticky for irregularly placed leaf fragments are also found glued to the surface. There is little doubt that the axis was originally cylindrical. It usually bears ovules on two sides of the compression, but in some specimens they occur in other positions. Some axes show definite scars which may belong to the bases of fallen ovules. If this is true, then the cone axis was covered by radially disposed ovules. No bract or any sterile appendage was seen in relation to the ovules and the axis. Some sterile linear bracts (or leaves?) may be seen crossing the exposed surface of the cone axis, but only in a few specimens, and I am not sure that they bear any relation to the ovules (Pl. 5, fig. 39).

The ovules are erect and show no covers or outgrowths. The integument is thick and possibly had some cell contents which formed the granules mentioned in the diagnosis. The nucellus is strongly cutinized down to near the base (chalaza), its cells near the base and apex being much shorter than at the middle. The anticlinal walls are also more strongly cutinized towards the base and apex.

The ovules still attached to the cone axis have some of their membranes preserved, and they were treated in the usual way with dilute alkali. They show the three membranes of the diagnosis, the inner and structureless one being the megaspore wall. The chalaza is clearly seen in some specimens, being somewhat elliptical and transversely elongated (probably the ovules were somewhat flattened). The scars seen on the axis are similar in size and shape and may correspond to the chalaza.

Detached seeds referred to *T. tigrensis* are preserved in two ways:

1. The stone is well developed within a cavity and shows the characteristic meshes on its outer surface. Usually no inner cuticle is preserved.

2. The seed is flattened as a disc from which good cutinized membranes can be obtained. The meshes on the outside are usually seen clearly. The stone is not preserved as a separate recognizable layer. Seeds still attached to the cone axis are always preserved in this manner.

Similar venation in the preservation of conifer seeds has been noted occasionally in other floras. Where the external meshes are seen clearly they distinguish the seed of *T. tigrensis* from that of the associated *Karkenia incurva* Archangelsky (1965).

These cones are identified with the foliage already described as *Trisacocladus tigrensis* for the following reasons: (1) there is one specimen which shows what I believe is an organic connection; (2) in the bed where these cones occur, only this type of foliage and male cones are known and no other plant remains have so far been found, among hundreds of vegetable fragments; (3) in a lower bed, where *Ginkgoites*

tigrensis is abundant, *Trisacocladus tigrensis* foliage and male and female cones also occur. (4) In another (Upper) bed which is probably a lateral equivalent to the *Trisacocladus* bed, distant about 700 metres from it, seeds of the cones and shoots plus male cones also occur together. Thus, these elements are associated in three different beds and there is one probable organic connection.

Discussion. In the absence of cuticle it is not possible to relate *Trisacocladus* with *Tomaxellia*, which occurs in the same formation but at different localities. There is agreement in the shape of leaves, although individual leaves of *Trisacocladus* are smaller. In *Tomaxellia* leaves spreading in one plane were not observed. All *Elatocladus* species described by Halle (1913*a*) from Hope Bay, Graham Land, are different. *E. heterophylla* is somewhat similar but differs in having leaves with an acute apex (on both short and long leaves) and in the variation of the size of the leaves found on different shoots (not so marked in *Trisacocladus tigrensis* as in *E. heterophylla*). There is also a difference in age, the Antarctic species being probably Middle Jurassic.

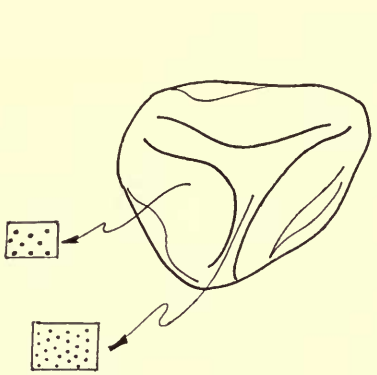
The male cones of *T. tigrensis* are of the type usually referred to the organ genus *Masculostrobus*. Several species of this genus are known from Jurassic and Cretaceous strata. Only one, *M. sahnii* Vishnu Mittre (1956) from the Jurassic of India, has pollen grains bearing three air bladders. The Indian cones are smaller (7 mm. × 3 mm.). Pollen grains usually bear 3 bladders, but 2 or 4 were also seen. The equatorial diameter of the grains is somewhat greater (32–39 μ against 12–32 μ in the present species). A few leaves on the basal portion of the cone of *M. sahnii* are known. They agree in shape with those of *Trisacocladus tigrensis*, but are smaller.

Vishnu Mittre (1957) considers that the female structures of *M. sahnii* probably belong to *Nipanioruha granthia* Rao discussed later. Pollen grains similar to those found in the cones, were observed in many preparations of dispersed pollen grains in sediments of other beds. They are commonly preserved with unexpanded air bladders and subtriangular equatorial outline. It is interesting to note that *Trisaccites* grains (like ours) are known from Upper Jurassic, Cretaceous and Early Tertiary sediments of Australia, New Zealand and Tasmania. The same geological range applies to *Microcachrydites*, another palynomorph, which has been found in the same localities and also in Antarctica (Cookson 1947).

Among Recent conifers *Trisacocladus* can be matched only within the Podocarpaceae. The leaves are similar to those found in *Podocarpus* and *Dacrydium*. Its male cones resemble in shape some cones of *Podocarpus*, but there is a clearly defined sporophyll axis in *Trisacocladus* instead of a more or less laminar microsporophyll found in Recent Podocarpaceae. On the other hand, pollen with three air bladders is found in some *Podocarpus* (e.g. *P. dacrydioides*), in *Microcachrys* and in *Microstrobos* (=*Phaerosphera*). The leaves of the two last genera are, however, different, being small and scale-like. It is noteworthy that in one species of *Phyllocladus* (*P. glaucus*), three air bladders are sometimes found in the pollen (Cranwell 1940).

In the Jurassic of Nipania (Rajmahal Series of India), many petrified coniferous remains have been described, some belonging to the Podocarpaceae. *Nipanioruha*

(as described by Rao 1946, and lately emended by Vishnu Mittre 1957) bears leaves comparable in shape with those of *Trisacocladus* and there is much more information available on the anatomy of these leaves which is lacking in our material. Male cones of the Indian genus are surrounded by leaves and therefore differ from *Trisacocladus* male cones which are shortly pedunculate and not covered by leaves. Both types of cones produce pollen with three air bladders.



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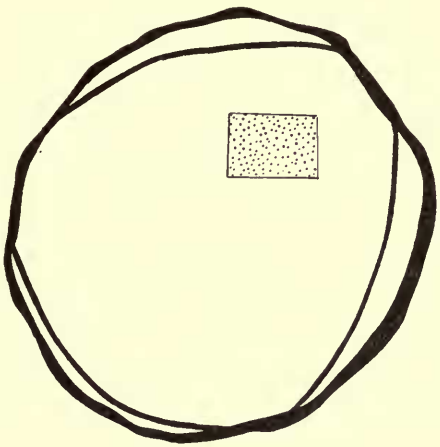

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FIG. 25. *Trisacocladus tigrensis* gen. et sp. n. Pollen grain showing three air sacs with their basal depressions. Slide LP 244, ×1100.

FIG. 26. *Apterocladus lanceolatus* gen. et sp. n. Pollen grain showing three rudimentary equatorial air bladders. Slide LP 242, ×1100.

Among fossil conifers, our female cones may be compared with *Mehtaia* Vishnu Mittre (1957), a Jurassic Podocarp from India. *Mehtaia* has erect ovules, no epimatium but small bracts. It differs, however, in its much thinner axis and in its markedly curved micropyle (straight in our material). Furthermore, the leaves of *Mehtaia* are different from those of *Trisacocladus*. All three species of *Mehtaia* have much smaller cones (the longest is 10 mm. against 20 mm. in *Trisacocladus*). Other female cones of the same formation from India differ in having inverted ovules (including those of *Nipanioruha granthia* Rao mentioned above), well developed bracts and sometimes also epimatia. As far as I am aware, there are no other similar female structures comparable with ours.

The affinity of the *Trisacocladus* cones is close to some Recent Podocarpaceae, but there are a few important differences (some probably due to lack of information about accessory structures in our material, such as the bracts). Recent Podocarpaceae have a well developed epimatium which covers the ovules to a varying degree. They also possess bracts in relation to the ovules. Our material may have bracts but no structure which could possibly suggest an epimatium. The ovules are thus naked. I believe that this structure (epimatium), if originally present, would surely

have been preserved together with the ovules in at least some of the numerous specimens examined. Although this is negative evidence, it is nevertheless suggestive.

Among living Podocarpaceae those having cones with erect ovules come closer to *Trisacocladus*. *Phyllocladus* and *Microstrobos* (=*Phaerosphera*) have erect ovules but also well developed epimatia (in *Phyllocladus* there is also an aril which, however, may be considered as a secondary feature). The cones of the living genera are usually smaller and have fewer ovules. *Microstrobos* is known only from Tasmania and South-east Australia. Recent *Phyllocladus* is known from New Zealand, Tasmania, Borneo and the New Guinea area. As a fossil it has been recorded from the Tertiary of Australia and New Zealand (Cookson & Pike 1954).

All characters of *Trisacocladus* (leaves, male and female cones) have been matched separately among living representatives of the Podocarpaceae. All other conifers may be excluded from consideration as they differ in their reproductive structures. The Recent genera *Podocarpus*, *Dacrydium*, *Microstrobos*, *Phyllocladus* and *Microcachrys* share some characters with the fossil form. Female cones with erect ovules are not known in *Podocarpus*, *Dacrydium* or *Microcachrys*. Pollen grains with three air bladders, on the other hand, are unknown in *Dacrydium* and unusual in *Phyllocladus* (and most species of *Podocarpus*). Long linear leaves are known only in *Podocarpus* and *Dacrydium*. It thus appears that no Recent genus of the Podocarpaceae shares all morphological characters with *Trisacocladus*. The Patagonian plant may well belong to a new genus of the family which became extinct in the Upper Mesozoic or Lower Tertiary. The geographical distribution of these plants was at least mainly gondwanic, being present in India, Australia, New Zealand, Antarctica and South America.

This assemblage constitutes an interesting stock of morphological characters from which many modern genera of Podocarpaceae may have arisen.

These considerations support the views expressed by Florin (1963) as to the origin and distribution of the Podocarpaceae in the past. The wide gap in our knowledge of this family in the Mesozoic is only partly filled by the impressions of leafy shoots, placed in noncommital genera such as *Pagiophyllum* or *Elatocladus*. But evidence is slowly accumulating in respect of this important family which must have played an outstanding role in southern lands. Our material shows how hazardous it may be to accept the presence of a living genus in old rocks on the basis of only one part of the plant. This is certainly the case with the leaves which are related to the living genus *Podocarpus*, and which may subsequently prove to have closer relationship with other members of the family, when fertile structures become available. The same may be said regarding the dispersed pollen in sediments. While it may definitely indicate a family link, it may also lead to erroneous conclusions when generic relations are established.

Genus ***APTEROCLADUS*** nov.

Derivation of name. *Aptero*, no wings, *cladus*, leaf.

Diagnosis. As for the only species, *Apterocladus lanceolatus* sp. n.

Apterocladus lanceolatus sp. n.

(Pl. 6, figs. 40–48 ; Pl. 7, figs. 52, 55 ; Pl. 8, figs. 68–70 ; Text-figs. 27, 28, 34)

Diagnosis. Woody plants. Lateral axis of penultimate order up to 2 mm. in diameter, bearing leafy branches at a wide angle, 8 mm. apart (seen in one specimen). Branchlets straight or slightly curved, longest seen (incomplete) 3 cm. × 1·5 mm wide (excluding leaves) or 1·7 cm. wide (including leaves). Leaves homomorphic bifacial, spirally disposed but expanded in approximately the same plane by twisting of the decurrent leaf bases. Leaves firm, coriaceous, entire and flat, straight, with one median vein, spreading 50–80°, lanceolate with acute apex, 6–8 mm. long × 1·5–2 mm. broad, maximum breadth near middle of blade, gradually tapering towards apex, abruptly contracted on base, broadly decurrent, each sheathing the axis for a distance of about 1·5–2 mm. downwards. Cuticle 2–3 μ thick. Stomata present on one cuticle, forming two bands near margins. Stomata in close bands, forming ill-defined rows, longitudinally orientated ; subsidiary cells of neighbouring stomata often in contact (lateral and polar); sometimes two stomata sharing a subsidiary cell.

Epidermal cells in stomatal bands usually tending to be isodiametric, sometimes rectangular. Epidermal cells on margins and middle of lamina usually rectangular or square, forming definite files. Epidermal cells on nonstomatiferous cuticle square or rectangular, forming definite files, all about 15–25 μ wide. Anticlinal cell walls unpitted, slightly sinuous, 2 μ thick. Surface wall finely granular. No papillae or hairs seen.

Stomata typically haplocheilic, monocyclic (sometimes imperfectly dicyclic). Stomatal apparatus oval. Guard cells slightly sunken, very feebly cutinized, surrounded by typically 5–6 subsidiary cells. Subsidiary cells may or may not be differentiated into polar and lateral. When differentiated, polar subsidiary cells usually square. Subsidiary cells sometimes with thickened surface wall. Mouth of pit oval or rectangular, with marked rim of cutin formed by fusion of subsidiary cells. Subsidiary cells sometimes with strong external cutin ridge parallel to mouth of pit, which may fuse with neighbouring thickening of adjacent subsidiary cells, forming a sort of ring. Hypodermis not cutinized.

Male cones shortly pedunculate, laterally attached to branches, oval, 0·6 × 0·35–0·5 cm. wide, with microsporophylls spirally inserted in central axis, close together, composed of main branch and distal (outer) leafy rhomboidal and acuminate head. More than one pollen sac present on each sporophyll.

Pollen grains sometimes with three rudimentary air bladders, almost spherical, sometimes a little flattened in polar axis. Equatorial diameter about 45 μ and polar diameter (flattened specimens) about 37 μ. Exine delicate, finely granular in texture and thinner on one half.

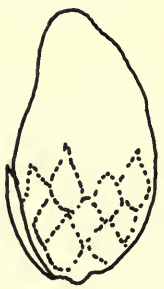
Holotype. LP 6296 (Bajo Grande, *Araucarites* bed).

Material. In addition to the holotype, LP 5665, 5666, 5698–5700, 5730, 5749 (Bajo Tigre, *Ptilophyllum* bed) ; LP 6302–6306, 6317–6327 ; BMNH, V.52282–93 (Bajo Grande, *Araucarites* bed). Slides LP 228–230, 242, 243, 245, 246 ; BMNH, V.52294–95 (Bajo Grande, *Araucarites* bed).

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, Bajo Grande, *Araucarites* bed and Bajo Tigre, *Ptilophyllum* bed, Santa Cruz Province, Argentina.

DESCRIPTION. *Apterocladus lanceolatus* is common in Bajo Grande, and occurs in the same bed as the other conifers *Araucarites minimus*, *Podocarpus dubius* and *Tomaxellia biforme*. Its preservation is similar, although the cuticle is not easy to prepare. The leaf is coaly and broken into small fragments which cannot be pulled out together. The largest fragments were treated with dilute alkali and then bits of cuticle were separated. However, the cuticle usually adheres very strongly to the rock matrix and better results were obtained by first dissolving the matrix with HF to free the cuticles. In both cases the cuticle appears very fragmentary but shows some diagnostic characters. One specimen (LP 6296) shows clearly a male cone in organic attachment to a leafy shoot. Pollen was obtained by scraping the organic remains on the microsporophylls. All grains are of one kind. Similar isolated male cones are abundant in the same bed. They all possess the same type of pollen grains and have therefore been included in the species. One of the isolated male cones (LP 6323) has a few compressed scale leaves at the base which after treatment with dilute alkali, showed very small fragments of cuticle with elongated epidermal cells. These cuticular fragments are similar to the leaf cuticle of *Apterocladus lanceolatus*. The cones are single or may be present in pairs (LP 6321, BMNH, V.52293).

Apterocladus lanceolatus also occurs abundantly in Bajo Tigre, in the *Ptilophyllum* bed (named here for the first time). These specimens lack a cuticle, but are otherwise identical. Only the impressions of square and rectangular epidermal cells can be seen, arranged in definite longitudinal files. Fragmentary remains, possibly belonging to this species were found in the Ticó Amphitheatre. (*Otozamites grandis* bed, LP 5149 and *Ticoa harrisii* bed LP 5370). One specimen yielded cuticle fragments with square or rectangular epidermal cells, arranged in files. One other speci-



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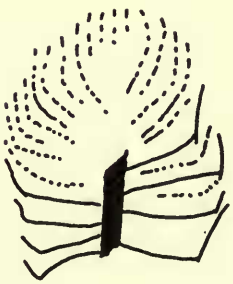

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FIGS. 27, 28. *Apterocladus lanceolatus* gen. et sp. n. Fig. 27. Male cone showing impressions of the outside of some microsporophylls and one leaf near base. BMNH. no. V.52291, ×8. Fig. 28. Male cone showing central axis and insertion of a few microsporophylls. LP 6326, ×8.

men from the *Taeniopteris* bed (LP 5279) shows a few leaves more than 1 cm. long, with tapering base and apex, one vein, but no cuticle is preserved. These fragments suggest that *A. lanceolatus* may be of widespread occurrence (it is over 50 km. from Ticó to Bajo Grande).

The pollen grains are interesting in that they have a clear equatorial thickening which is sometimes trilobed. These lobes may well represent incipient air sacs, in which case there is further evidence for including *Apterocladus* in the Podocarpaceae. Many similar pollen grains found detached in the sediments show this character. A detailed study of the pollen grains has been published by Gamerro (1965).

Discussion. *Apterocladus lanceolatus* differs from all other conifers so far studied in the Ticó flora. The leaves are only comparable to *Podocarpus dubius* although there are many differences in shape and in cuticular structure. Stomata of both species are placed in bands, always longitudinally orientated, with oval or rectangular mouth of pit. These characters definitely indicate a Podocarpaceous affinity. Some Taxodiaceae have leaves of similar habit, but usually they are amphistomatic. Moreover, the orientation of stomata in Taxodiaceae is irregular (they may be longitudinally, obliquely or transversely orientated). Only *Sequoia*, *Taxodium* and *Glyptostrobus* have leaves of similar habit to *Apterocladus*.

The pollen grains of *A. lanceolatus* differ from those of Taxodiaceae in the lack of a papilla-like germinating pore. In this respect they are more like those of Recent Araucariaceae, although presenting some differences in the structure of the exine. Most Recent Podocarpaceae have markedly winged pollen grains, and therefore differ from our species. Only *Saxegothaea* resembles our species in having wingless grains, but the exine structure is rather different and the size of the grains is smaller in the Recent genus. The vegetative part of *Saxegothaea* also bears some resemblance to our fossil. The leaves are, however, much longer (although contracted at the base) while the male cones are shorter than those of *Apterocladus*. The cuticular structure is similar in that *Saxegothaea* bears stomata on one epidermis, placed in two bands and longitudinally orientated. However, in the Recent genus the stomatal rows are better defined than in *Apterocladus*. Finally, epidermal cells in the Recent genus although rectangular and placed in files, have markedly sinuous walls, a character lacking in *Apterocladus*. Nevertheless, *Apterocladus* appears to be more closely related to *Saxegothaea* than to any other living conifer. This genus is now known in the Patagonian Andes (Chile and Argentina), not far from where the Baqueró Formation is exposed (less than 500 km.). It may be worth mentioning that *Saxegothaea* has been recorded from the Oligocene of Fueguia (about 700 km. southwards), although there is some doubt about Dusen's determination (1899).

The pollen grains of *Apterocladus* may well be compared (or confused) with some *Araucaricites* found in dispersed condition. Its grains have the equatorial thickened zone which might represent incipient sacci, and the thinner exine of one of the halves might represent a colpus. Thus a winged grain may be derived from *Apterocladus*, such as the grains of *Phyllocladus*, some of which have very small incipient sacs. On the other hand, the incipient sacci could represent a step in a reductionary series,

in which case the next step would be represented by non-saccate grains (as in *Saxegothaea*).

The contracted leaf bases of *Apterocladus* distinguish it from all the species of *Elatocladus* described by Halle (1913*a*) from the Jurassic of Graham Land. There may be some resemblance to *Elatocladus* sp. figured by Halle (1913, pl. 5, fig. 8) from the Lower Cretaceous of Rio de los Fosiles, Santa Cruz ; but here the contraction at the base of the leaves is gradual, while it is more marked in *Apterocladus*.

Coronelia molinae Florin (1940), from the Tertiary of Chile shares with *Apterocladus* the character of contracted leaf-bases, although in the Chilean species this constriction is much more pronounced. There are also differences in cuticular structure, mainly in the presence of papillae and peculiar hairs in *C. molinae*.

There is some resemblance to the two species of *Palissya* described by Frenguelli (1949) from the Upper Jurassic of Chubut Province, Argentina. The leaves are similar and have contracted bases, but nothing is known about their cuticular structure.

Genus ***PODOCARPUS*** L'Héritier

Podocarpus dubius sp. n.

(Pl. 6, figs. 49, 50 ; Pl. 7, figs. 53, 54 ; Text-figs. 29–33)

Diagnosis. Woody plants. Lateral axis of penultimate order up to 3·5 mm. in diameter, bearing leafy branchlets at an angle of about 45°, 1–1·5 cm. apart (in a row). Branchlets usually straight, sometimes slightly curved, longest seen (incomplete) 4 cm. × 2 mm. (not including leaves) or 2 cm. wide (including leaves). Leaves dimorphic. Large leaves usually of bilateral type, spirally disposed, linear, straight or falcate, spreading (40–80°), tapering to acute or acuminate apex, with uncontracted, markedly decurrent base, sheathing axis for about 4–5 mm., uninerved, largest 1·3 cm. × 1·5 mm. broad in free portion. Short leaves usually situated at base of branchlets or near apex, or on branches of penultimate order ; they are spirally disposed, adpressed to axis or spreading in all directions, markedly decurrent (decurrent sector sometimes larger than free part of leaf). Short leaves may occasionally be placed among long leaves. Both cuticles of same thickness, about 3–4 μ. Stomata present on both cuticles, few on decurrent sector and forming ill-defined rows. In middle sector of leaf, stomata placed in two well defined bands per epidermis, tending to be near margins leaving a conspicuous median sector devoid of stomata (this sector may correspond to real lateral margins of the leaf). Stomata in bands, forming more or less defined longitudinal rows, longitudinally orientated, sometimes obliquely, never transversely. Stomata of a row sometimes with subsidiary cells in contact, but never shared.

Epidermal cells in stomatal bands isodiametric or elongated, with rounded contours. Square or rectangular epidermal cells on same rows as stomata. Those on margins and middle of lamina typically rectangular, about 20 μ wide, placed in files. Median longitudinal sector sometimes occupied by markedly elongated rectangular cells. Cell walls straight, unpitted, 3–4 μ thick, with finely granular surface. Round delicate papillae, occupying most of cell surface, sometimes seen.

Stomata haplocheilic, monocyclic to imperfectly dicyclic. Stomatal apparatus oval. Guard cells slightly sunken, very feebly cutinized, surrounded by typically 4–5 subsidiary cells. Subsidiary cells occasionally with cutin ridges parallel to mouth of pit. Polar subsidiary cells sometimes differentiated, when differentiated usually square. Mouth of pit oval, sometimes rectangular, constricted by a strong rim of cutin formed by fusion of subsidiary cells. Rim of cutin of stomata less conspicuous in one of the two cuticles. Hypodermis not cutinized.

HOLOTYPE. LP 6309.

MATERIAL. In addition to the holotype, LP 6307–13, 6414–29 ; LIL 2753–62 ; BMNH, V.52296–99. Slides V.52300–01 ; LP 221–227.

HORIZON AND LOCALITY. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed. Estancia Bajo Grande, Santa Cruz Province.

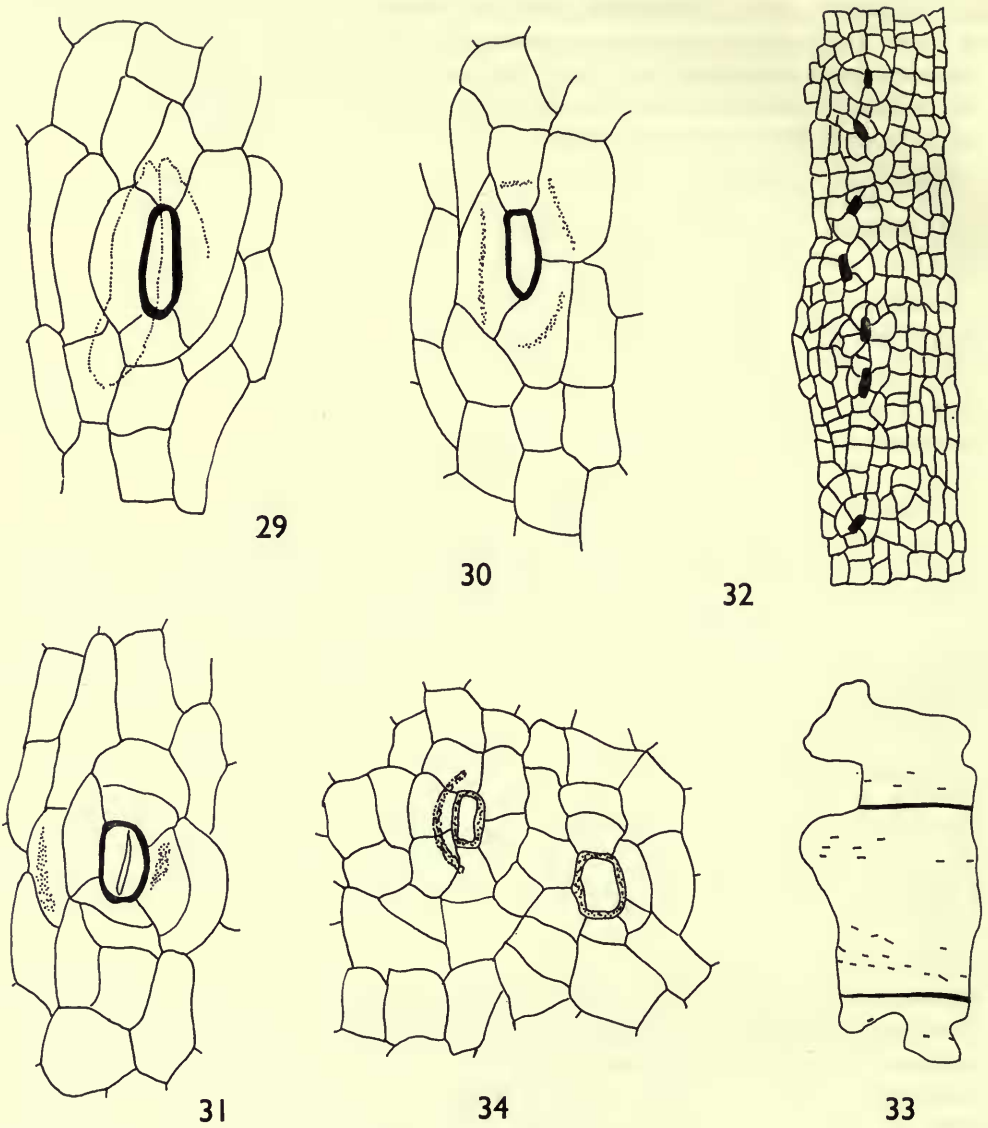
DESCRIPTION. This is one of the commonest species in the *Araucarites* bed of the Bajo Grande locality. The substance of the leaves is coaly and broken into small fragments which can be treated with dilute alkali in order to obtain small bits of cuticle. The leaves of most specimens examined are usually of the long type, and in one rank of a branchlet their length may vary considerably. Short leaves were seen in a few specimens ; they usually occur at the base of branches. Unfortunately it was impossible to obtain cuticular fragments from these small leaves. Long leaves are considered to be of the bilateral type because there is no evidence of torsion at the base and yet they tend to be disposed in one plane. The base of these leaves is wide and they sheath the axis for a considerable distance. Following Laubenfels's classification of coniferous leaves (1953) they fall into his type I, tetragonal in cross-section and falcate in profile.

Stomatal bands are clearly defined. Although only small portions of cuticle were obtained I believe that there are more stomata in the bands of the lower cuticle, especially on the unexposed surface. Text-fig. 33 shows a sector of a long leaf. The two black lines may correspond to a keel and thus the stomatal bands between these lines correspond one to half the lower cuticle and the other to half the upper cuticle.

DISCUSSION. This species differs clearly from all conifers so far studied in the Ticó flora. *Tomaxellia degiustoi* is the one which comes closest, but it differs in leaf arrangement (radially disposed and not spreading in one plane). Also the cuticular structure is different ; in *Tomaxellia* stomatal bands have no definite stomatal rows.

There is some resemblance to *Elatocladus conferta* (Oldham) from the Jurassic of Hope Bay (Halle 1913*a*), although the leaves of *Podocarpus dubius* sp. n. are usually longer. Florin (1940 : 31) considers *E. conferta* to be similar to Recent *Podocarpus* of the *Eupodocarpus* section. *Elatocladus jabalpurensis* (Feistm.) and *Elatocladus* sp. (Halle 1915*a*, pl. 9, figs. 7–9) may also be compared with our species. Florin (1940) considers these two species as *Podocarpus*, subgenus *Stachycarpus*.

Frenguelli (1949) described some fertile specimens of probable Jurassic age from the Canadón Asfalto, near Paso de los Indios in the Chubut Province. These plants



FIGS. 29–33. *Podocarpus dubius* sp. n. Figs. 29–31. Stomata. (Fig. 29, slide LP 225. Fig. 30, slide LP 226, Fig. 31, slide LP 221). All ×370. Fig. 32. A stomatiferous row on lower cuticle. Slide LP 225, ×85. Fig. 33. Disposition and orientation of stomata on a bilateral leaf (upper half, probably upper cuticle). Slide LP 226, ×30.

FIG. 34. *Apterocladus lanceolatus* gen. et sp. n. Two stomata. Slide LP 228, ×370.

were referred to *Palissya conferta* (Oldham) and *Palissya jabalpurensis* Feistm. Both species differ from ours in their contracted leaf bases. The female cones, judging from Frenguelli's illustrations (1949, pls. 1, 2) are rather obscure structures. His reconstruction of the cone scales (text-fig. 1) is tentative and must be critically considered. All previous references of *Palissya* from India have been discarded. Most of the species have been included in the artificial genus *Elatocladus* in order to differentiate them from typical species of *Palissya* better known from shoots and female cones in Europe (Florin 1963). This *status* should be accepted until better material of the Gondwana floras becomes available. Frenguelli's specimens would be better placed in the genus *Elatocladus*.

Podocarpus? *palissyafolia* (Berry) Florin from the Baqueró Formation in Cerro Cuadrado and Punta del Barco was originally described as *Elatocladus palissyafolia*, on the basis of a fragmentary specimen (Berry 1924). It differs from *Podocarpus dubius* in the contracted leaf bases but is similar in other respects. The leaves are not bilateral as in our species. Unfortunately, this material is too fragmentary for exact identification and no new material is available from the type localities.

Podocarpus inopinatus Florin, from the Tertiary of Chile, has similar but smaller leaves (4–7 mm. long against up to 1·3 cm. long in our species). There is general agreement in cuticular structure: the leaves are amphistomatic, with marginal bands of stomata and epidermal cells arranged in rows. However, in *P. inopinatus* neighbouring stomata may share a polar subsidiary cell, but this has not been observed in our material. Moreover the Chilean species has dicyclic stomata while *P. dubius* has monocyclic to imperfectly dicyclic stomata. Pitting of the anticlinal cell walls reported for the Chilean species is unknown in our material. *Podocarpus inopinatus* belongs to the section *Dacrycarpus* of the genus (according to Florin). The other two species of *Podocarpus* described by Florin in the same paper differ in the shape and insertion of their leaves, and in cuticular structure.

Among the Indian species of *Elatocladus*, there are two with bilateral leaves similar to those of *P. dubius*. In *E. plana* (Feistmantel 1879, Seward 1919, text-fig. 802, Sahni 1928) the leaves are much longer and disposed closer to each other. *E. tenerrima* (Feistmantel 1877, Sahni 1928) differs in the typically wide angle of insertions of leaves (almost perpendicular to the branches); in *P. dubius*, the leaves normally form an acute angle with the branch. Both Indian species may, however, be closely related to *P. dubius* in having bilateral and amphistomatic leaves.

So far as comparison with living conifers is concerned, *Podocarpus dubius*, having bilateral leaves may be closely compared with the Podocarpaceae. Among the family, this condition is known to occur in the genera *Acmopyle*, *Dacrydium* and *Podocarpus* sect. *Dacrycarpus*. I believe that our species in leaf morphology and cuticular structure is better placed in *Podocarpus*. Lacking other characters, this combination is to be preferred (following Florin's (1940) paper on Tertiary material from Chile). The difference in age is, however, considerable and I am not sure that our species really belongs to *Podocarpus* as we know it from Recent material.

The main difference between *Podocarpus dubius* and other genera with similarly shaped leaves is the bilateral condition of the leaves in *P. dubius*, not found in any

other families except the Podocarpaceae. The arrangement of stomata in bands is a common character in both Podocarpaceae and Taxodiaceae, but in the former, more or less well defined files of stomata occur in bands as they do in *P. dubius*. On the other hand all living Taxodiaceae are exclusive to the Northern Hemisphere, with the exception of *Athrotaxis*, which is clearly different from our species and is known living and fossil from the Southern Hemisphere. Among Araucariaceae there are no similar species, all possess leaves of one kind (with no foliar dimorphism).

Podocarpus dubius may be considered as another fossil member of the Podocarpaceae which inhabited Patagonia during Lower Cretaceous times.

Genus ***TOMAXELLIA*** Archangelsky 1963 : 86

Emended diagnosis. Woody plants with branches up to the fourth order. Leaves decurrent, spirally inserted, homomorphic (long) or dimorphic (long and short). Long leaves narrow, ending with acute apex, widest at their decurrent part, rhomboidal in transverse section, with sharp lateral angles.

Cuticle thick. Stomata present on both cuticles. On lower cuticle, at base of leaves stomata irregularly distributed and indistinctly orientated ; stomata forming irregular bands in middle of lamina. On upper cuticle stomata usually forming two bands from base to near apex. Orientation of stomata on free part of both cuticles oblique to longitudinal, sometimes transverse. Rows of stomata in bands ill-defined. Stomata when in a row usually separated, sometimes with outer encircling cells in contact, never sharing subsidiary cells. Epidermal cells between stomatal bands, rows and margins elongated, rectangular.

Stomata similar on both cuticles, monocyclic to dicyclic. Stomatal apparatus oval or circular (never rectangular). Guard cells sunken in a pit, surrounded by typically 4–5 subsidiary cells. Hypodermal cells cutinized, markedly elongated.

Discussion. Only one species of *Tomaxellia* (*T. degiustoi*) has so far been described (Archangelsky 1963). New material from Bajo Grande includes a new species, *T. biforme*, and this together with additional specimens from the type locality in Ticó Amphitheatre are described below Comparisons have already been made with Recent genera of Araucariaceae, Taxodiaceae and Podocarpaceae, and with the fossil genera *Elatides* and *Elatocladus*.

Vishnu-Mittre (1957) described a new genus, *Indophyllum* for shoots having leaves with free margins of lamina extending beyond the leaf cushion (as in *Pagiophyllum*) but they are homomorphic and much shorter than in *Tomaxellia*. One of his three species, *Indophyllum raoi*, has leaves which are rhomboidal in cross-section. In all three species, the stomata are longitudinally orientated. Only in *I. raoi*, on the lower cuticle, are the stomata irregularly orientated but they are longitudinally orientated on the upper epidermis and therefore differ from *Tomaxellia*. No detailed comparison of the stomatal structure is possible, because many characters are not preserved in the Indian material. *Indophyllum* is of Upper Jurassic age. Other leaves described from the same formation differ in having definite Podocarpaceous characters such as orientation of stomata in bands and stomatal structure.

Tomaxellia degiustoi Archangelsky

(Pl. 4, fig. 17)

1963 *Tomaxellia degiustoi* Archangelsky : 87, pl. 7, figs. 39, 40 ; pl. 8, figs. 58–60 ; pl. 11 ; pl. 12, fig. 79 ; text-figs. 72–74.

The new material collected in 1962 from the *Ticoa harrisii* bed in the Ticó Amphitheatre, yielded some good fragments of this species. When originally described, *T. degiustoi* was based on two very small fragments of branchlets and isolated leaves found in the rock matrix. With these new specimens knowledge of the gross morphology of branches and branchlets is now available. The leaves are spirally disposed on the branches and do not spread in one plane, as they do in many of the Podocarpaceae. The angle formed by the leaves with the axis is always very acute (never more than 45°), usually about 20–30°. Sometimes the leaves are almost adpressed to the axis. The broadest branches seen show clearly the oval scars of the leaf cushions. The branchlets are irregularly disposed on the branches, and may be widely separated or almost opposite. The cuticles are identical with those of typical material.

The original diagnosis has been enlarged in respect of the external morphology, the rest has been left unchanged.

Emended diagnosis. Woody plants. Branches straight or slightly curved, 3 mm. in diameter, longest seen 11 cm. (base and apex truncated) bearing irregularly inserted branchlets at distances varying from 1–3·5 cm. Branchlets forming acute angle with branch (about 10–50), straight or slightly curved, 4–5 cm. long (incomplete) bearing homomorphic leaves spirally inserted and spreading at acute angle or tending to be adpressed to axis. Leaves falcate, long and narrow, slightly decurrent, almost acicular, up to 1·3 cm. long × 1·5 mm. wide, ending with acute apex. Leaves broadest at base, gradually tapering towards apex. Leaf cushion on branches large, persistent, up to 8 mm. long × 2·5 mm. broad. Leaf cushions on branchlets small, oval or rhomboidal, 2 mm. long × 1 mm. broad. Free part of leaf rhomboidal in transverse section, but upper and lower angles somewhat rounded ; in middle region of leaf lower angle bearing wide short papillae. Lateral angles sharp, entire.

Cuticle as for original diagnosis.

Material. In addition to the material quoted in 1963 ; LP 5052, 5059, 5117, 5342.

Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member, *Ticoa harrisii* bed. Estancia La Magdalena, Ticó Amphitheatre, Santa Cruz Province, Argentina.

Tomaxellia biforme sp. n.

(Pl. 4, figs. 18–20 ; Pl. 7, fig. 51 ; Text-figs. 35–39)

Diagnosis. Main branches 3 mm. wide, giving off in different planes numerous lateral branchlets of a second order, up to 6 cm. long ; these branches give off at

acute angle lateral shoots of a third order, which may branch once again to give branchlets of ultimate order. Leaf cushions small, oval or rhomboidal, about 1·5 mm. long × 1 mm. broad. Leaves spirally disposed, mainly of two kinds : (1) short, with rounded apex and adpressed to axis, and (2) long, linear, with acute apex, with free part spreading outwards at almost right angles. Longest leaf, 4·7 mm. × 2 mm. wide ; shortest, 1·5 mm. × 0·8 mm. wide. Length-breadth ratio from 4·3 : 1 to 1·6 : 1. Leaves widest at their decurrent part (on leaf base cushion). Apex of leaves may project towards the stem. Leaves in section probably rhomboidal, with sharpened lateral angles and rounded lower angle ; upper angle not prominent. Veins not seen.

Cuticle 4–5 μ thick. Stomata present on both cuticles. On lower cuticle, at base (decurrent sector) stomata irregularly distributed and variably orientated ; in middle of lamina forming two irregular bands near lower angle which becomes thinner towards apex. Stomata on upper cuticle forming two bands from base towards apex, leaving clearly two marginal and one central sector devoid of stomata. Orientation of stomata on both cuticles tending to be oblique or longitudinal. Two marginal sectors, 10–15 cells wide, devoid of stomata and clearly marked on lower cuticle. On both cuticles, rows of stomata in stomatal bands may be present ; usually not well defined. Stomata present near apex on both cuticles. Stomata when in a row, usually separated, sometimes with outer encircling cells in contact, but never sharing subsidiary cells. Epidermal cells on base (decurrent sector) about 30–35 μ in diameter, isodiametric (square or with rounded contours). Epidermal cells in stomatal bands isodiametric or rectangular (longitudinally or transversely orientated). Epidermal cells towards margins becoming more rectangular, longitudinally orientated, up to more than 100 μ long. On margins, where both cuticles join, epidermal cells project outwards, forming a serrate edge with free apices of cells, this character being more prominent in smaller leaves, and almost non-existent in larger leaves. Cell surface flat, with no trichomes or papillae, sometimes faintly granular. Anticlinal walls straight, unpitted, strongly cutinized down to hypodermis, about 5 μ thick.

Stomata similar on both cuticles, typically imperfectly monocyclic to dicyclic. Stomatal apparatus usually oval or circular (never rectangular). Guard cells sunken in a pit, very feebly cutinized, surrounded by typically 4–5 inner subsidiary cells more or less isodiametric, finely striated, forming mouth of pit, slightly sunken below general epidermal surface. Outer encircling cells strongly cutinized with inner lateral walls slightly overhanging depression of the epistomatal chamber.

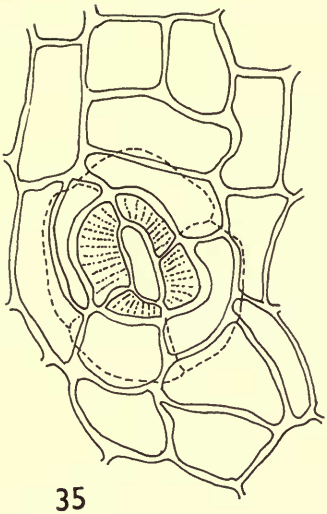
Hypodermal cells cutinized, markedly elongated.

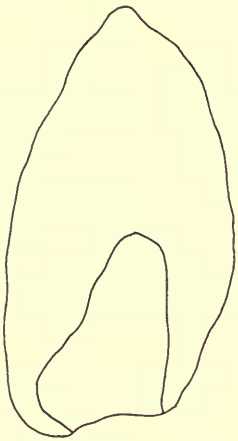
Holotype. LP 6278.

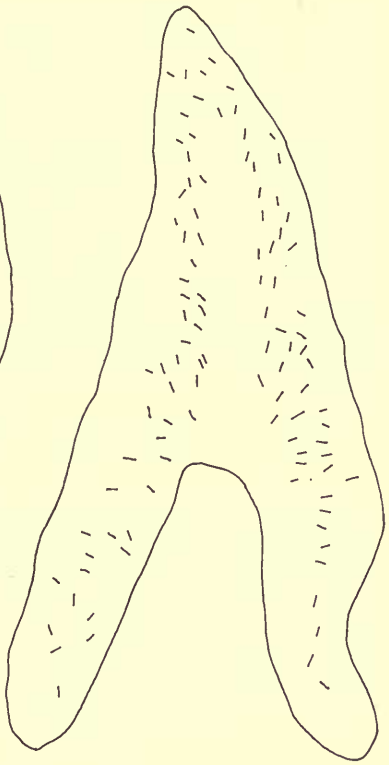
Material. In addition to the holotype, LP 6279–80, 6283–87, 6289–93, 6297 ; BMNH, V.52279–82. Slides LP 199–218 ; BMNH, V.52283–86.

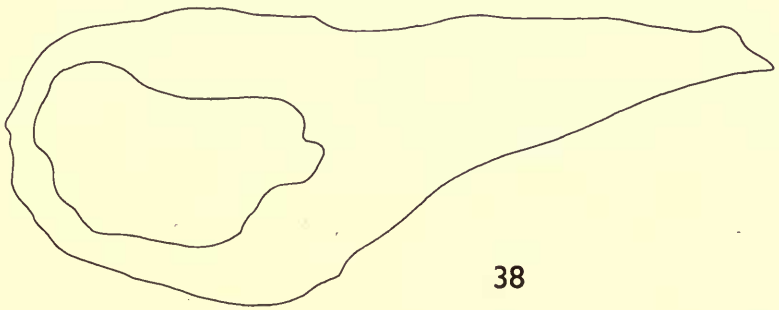
Horizon and locality. Lower Cretaceous, Baqueró Formation, lower member, *Araucarites* bed ; Estancia Bajo Grande, Santa Cruz Province, Argentina.

Description. This is a very common species in the *Araucarites* bed of Bajo









FIGS. 35–39. *Tomaxellia biforme* sp. n. Fig. 35. Stoma. Slide LP 202, ×370. Fig. 36. Section of a stoma, ×370. Fig. 37. A short leaf. Slide LP 200, ×30. Fig. 38. A long (normal) leaf. Slide LP 199, ×30. Fig. 39. Distribution and orientation of stomata on upper epidermis. Slide LP 202, ×30.

Grande. The leaves are usually of the long type, but short leaves are not uncommon ; this short type may occur singly or in groups or series, followed by series of longer leaves. This dimorphism is known to occur among both fossil and Recent conifers. There is great variation among the leaves of this species, but they are alike in cuticular structure, and in stomata in particular. The distribution of stomata on the upper epidermis is characteristic ; at the base of the leaf they tend to be transversely orientated. On the lower cuticle, stomata may be present directly on the lower angle or else there may be a zone devoid of stomata. Epidermal cells are usually devoid of papillae, but in one specimen (LP 6286) several leaves showed papilla-like cutin thickenings on the apical sector of the lower cuticle, occurring on the transverse anticlinal walls of rectangular cells. Also in these specimens, the lateral serrate margins are more conspicuous than in other forms of the species, but this is a varying character. Stomatal apparatus is alike in all specimens examined. Sometimes 6 subsidiary cells are present, but usually there are 4–5. The striation of inner subsidiary cells is constant, and the striae tend to be placed transversely to the mouth of the pit.

ACKNOWLEDGMENTS

I would like once more to express my sincere thanks to Professor T. M. Harris (Reading University) for many important suggestions, and to Mr. F. M. Wonnacott (British Museum, Natural History) for critically revising the manuscript. I am also indebted for aid in field excursions to the National Oil Company of Argentina (YPF). Mr. L. Ferreyra of the La Plata Museum took the photographs of the material, and Mr. J. C. Gamerro supplied the photographs of the pollen grains, included in the present paper.

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PLATE 1

Pachypteris elegans sp. n.

FIG. 1. General aspect of holotype. LP 6233, ×1.

Ticoa lamellata sp. n.

FIG. 2. General aspect of holotype. LP 6250, ×1·3.
FIG. 8. Lower cuticle (middle) and upper cuticle (right). Slide LP 174, ×30.
FIG. 9. Lower cuticle showing distribution of stomata and small hair bases. Slide LP 174, ×100.

Almargemia incrassata sp. n.

FIG. 3. Fragmentary pinnae. Left, BMNH, no. V.52664; right, LP 6254, ×1·3.
FIG. 4. General aspect of holotype. LP 6255, ×1·3.

Araucarites baqueroensis sp. n.

FIG. 5. General aspect of holotype. LP 5766*b*, ×1.

Araucarites minimus sp. n.

FIG. 6. General aspect of holotype. LP 6329, ×3.
FIG. 7. A small scale showing acuminate apex. LP 6330, ×3.

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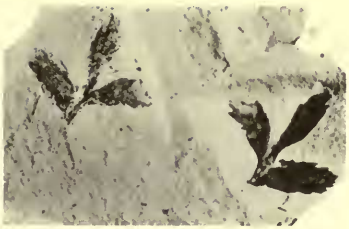

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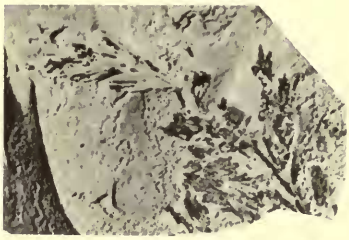

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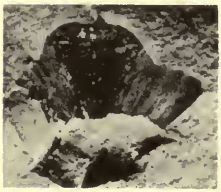

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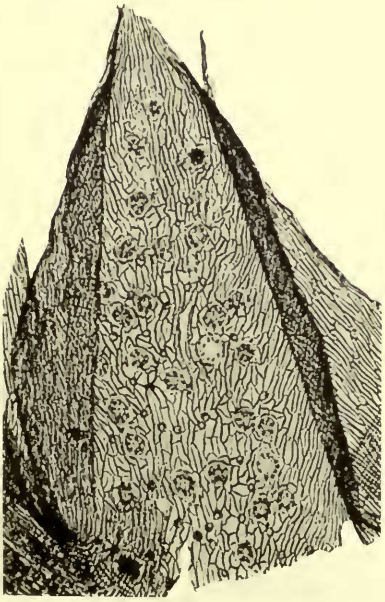

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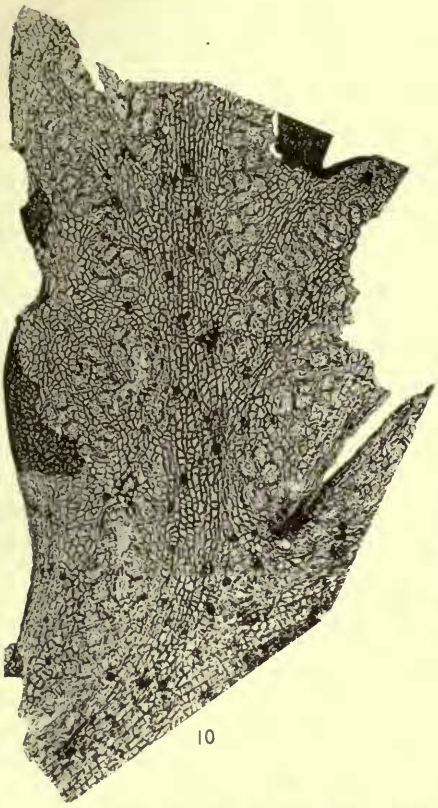
PLATE 2

Pachypteris elegans sp. n.

FIG. 10. Lower cuticle of undifferentiated pinna, showing distribution of stomata and venation. Slide LP 169, ×30.

FIG. 11. Lower and upper cuticles of a pinnule. Slide LP 170, ×30.

FIG. 12. Stomata on lower cuticle. Slide LP 169, ×500.



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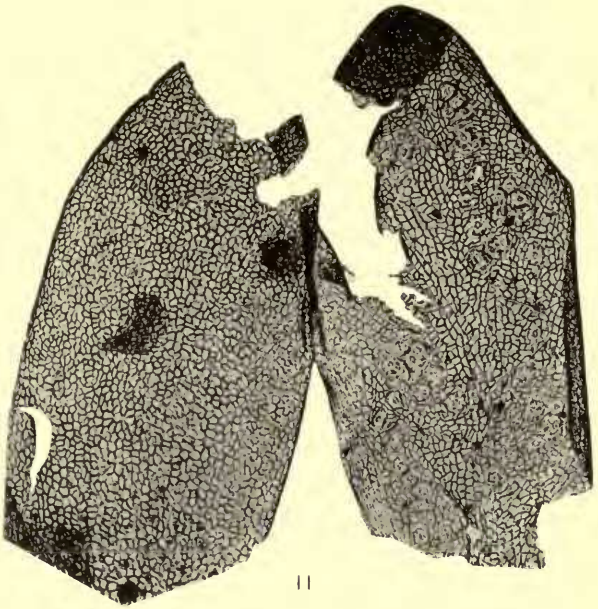

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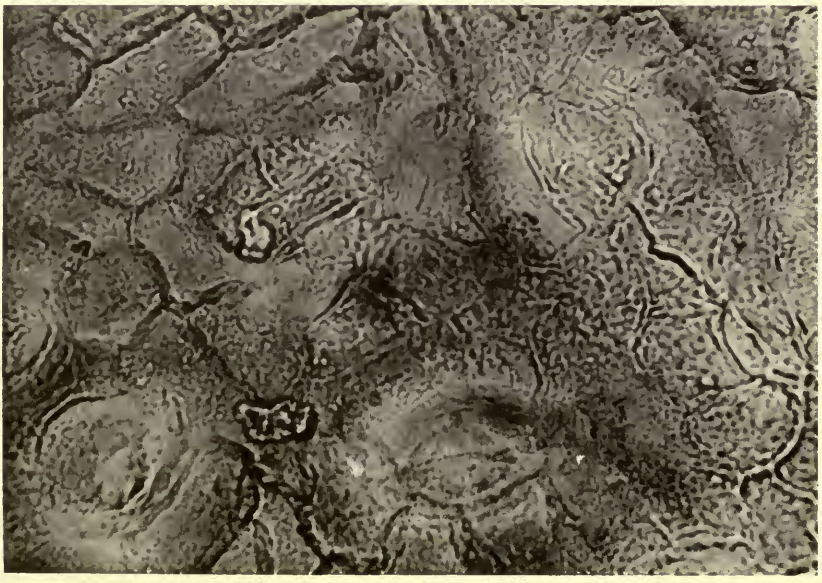

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PLATE 3

Almargemia incrassata sp. n.

FIG. 13. Lower cuticle (left) and upper cuticle (right) showing two types of epidermal cells. Slide LP 184, ×100.

FIG. 14. Lower cuticle showing stomata. Slide LP 184, ×500.

Ticoa lamellata sp. n.

FIGS. 15, 16. Stoma focused at two different levels. 15, mouth of pit; 16, guard cells. Slide LP 174, ×500.

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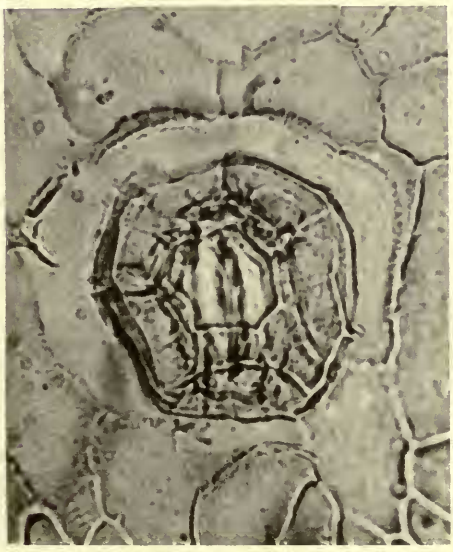

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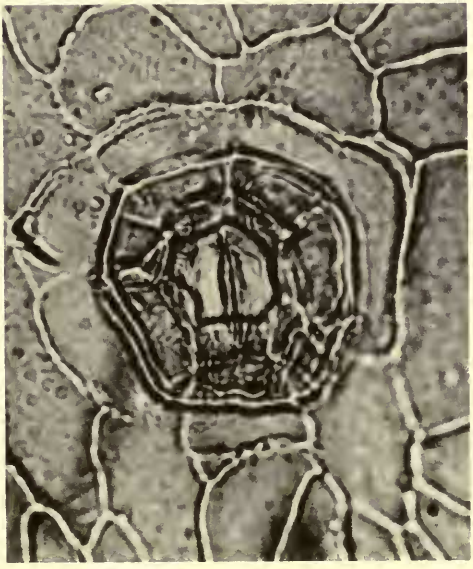

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PLATE 4

Tomaxellia degiustoi Archangelsky

FIG. 17. Branched specimen. LP 5117, ×1·3.

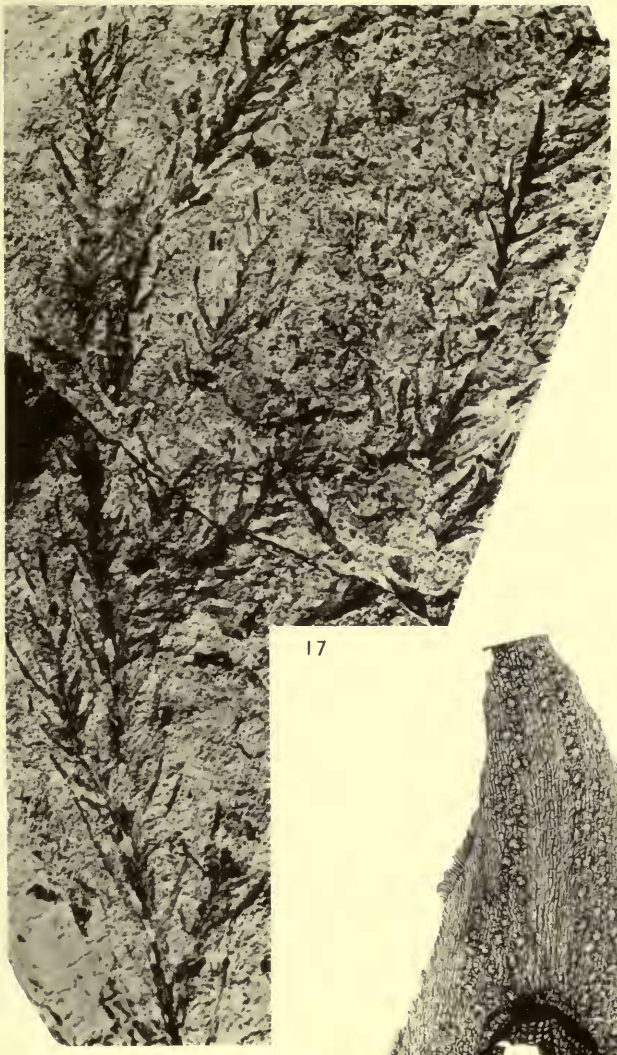
Tomaxellia biforme sp. n.

FIG. 18. General aspect of holotype. LP 6278, ×0·75.

FIGS. 19, 20. Lower (19) and upper (20) cuticles, showing distribution of stomata. Slide LP 202, ×30.

Trisacocladus tigrensis gen. et sp. n.

FIG. 21. Two fragmentary branches. LP 5845, ×1.



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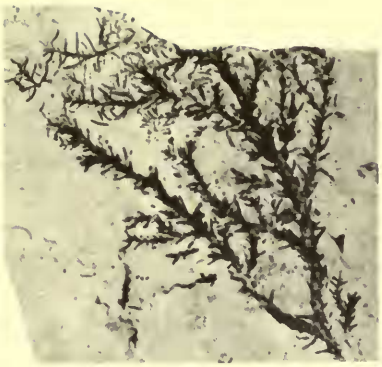

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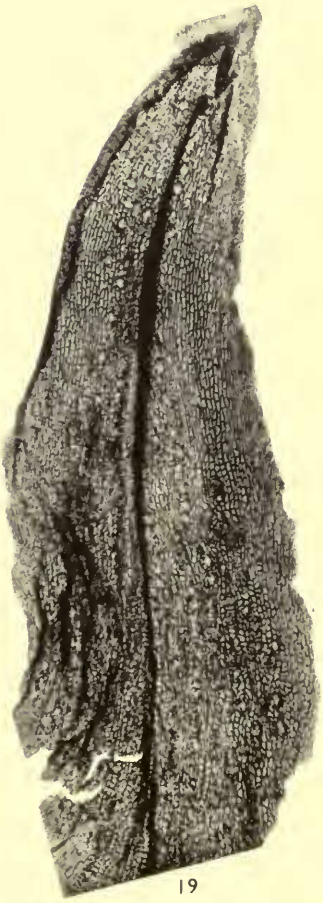

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PLATE 5

Trisacocladus tigrensis gen. et sp. n.

FIG. 22. Same specimen as Fig. 21, ×3.

FIG. 23. Branched twig with leaves spreading in one plane. LP 5827, ×1·5.

FIG. 24. Holotype. Pollen sacs are seen as paler structures among microsporophylls. LP 5826, ×1·5.

FIG. 25. The same, ×4.

FIGS. 26–28. Male cone, three different magnifications, showing microsporophylls. LP 5829, ×1, ×3, ×8.

FIGS. 29, 30. Wide branch showing leaf scars. BMNH. no. V.52238, ×1 and ×3.

FIGS. 31, 32. Branch with female cone, showing probable attachment. LP 5846. Fig. 31, ×1 and Fig. 32, ×3. *ca*, cone axis; *o*, ovules still attached to cone axis.

FIG. 33. A detached seed. LP 5847, ×10.

FIG. 34. A cone axis showing irregular scars. LP 5842, ×1.

FIGS. 35–37. Cone showing axis and a few ovules laterally attached. LP 5838, ×1 and ×3; counterpart LP 6231, ×2. The white dots are remnants of megaspores.

FIG. 38. Cone axis and attached ovules. LP 6218, ×2.

FIG. 39. Cone axis with probable bracts (?) transversely disposed. LP 6215, ×2.

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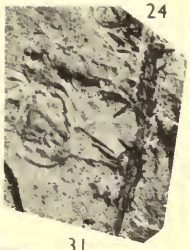

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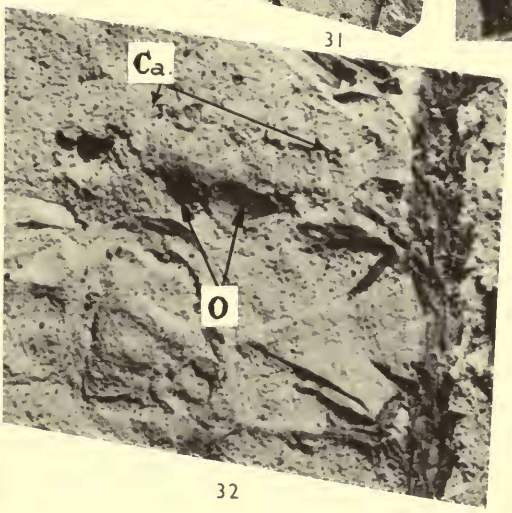

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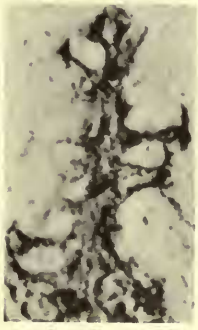

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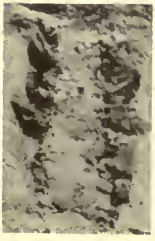

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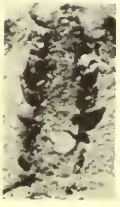

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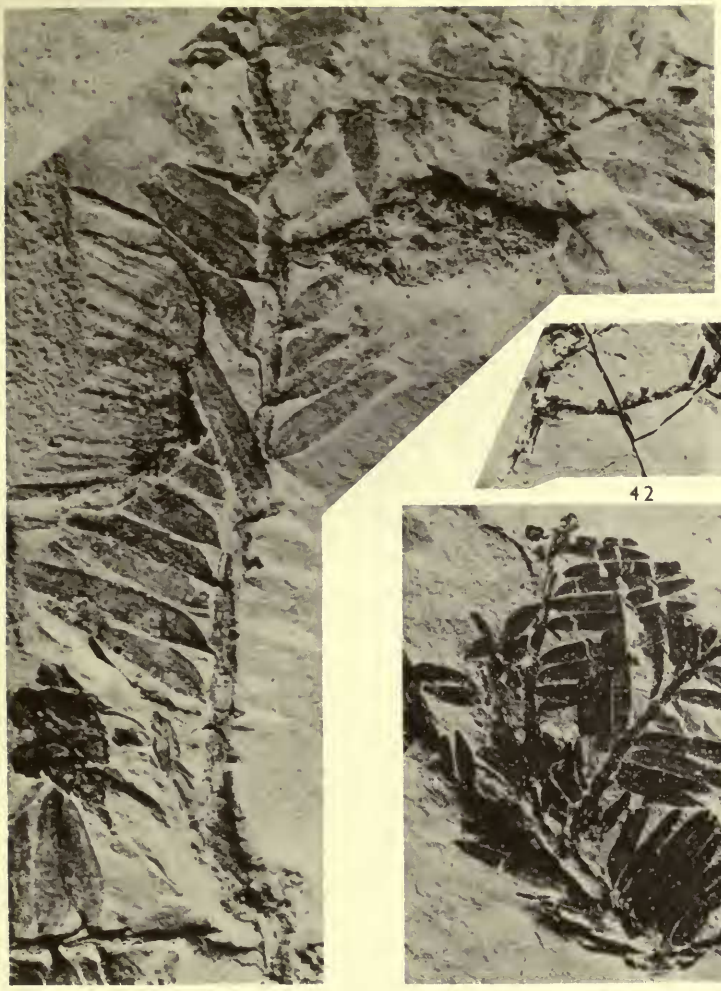
PLATE 6

Apterocladus lanceolatus gen. et sp. n.

FIG. 40. Holotype, showing attached male cone. LP 6296, ×1.
FIG. 41. Same, ×3.
FIGS. 42–44. Branched specimens. Fig. 42, LP 6302, ×1; Fig. 43, LP 6304, ×2; Fig. 44, LP 6303, ×1.
FIGS. 45, 46. Male cone showing external surface of microsporophylls. BMNH. no. V.52291, ×3 and ×8.
FIGS. 47, 48. Twin male cones. LP 6321, ×1 and ×3.

Podocarpus dubius sp. n.

FIG. 49. A branch. LP 6302, ×1.
FIG. 50. The holotype. LP 6309, ×1.



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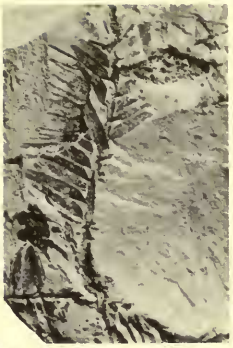

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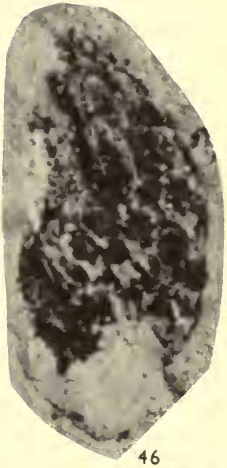

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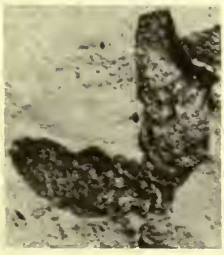

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PLATE 7

Tomaxellia biforme sp. n.

FIG. 51. Stomata of upper cuticle. Slide LP 202, ×500.

Apterocladus lanceolatus gen. et sp. n.

FIG. 52. Stomata in a band. Slide LP 228, ×500.

FIG. 55. General aspect of upper non-stomatiferous (left) and lower stomatiferous (right) cuticles. Slide LP 228, ×100.

Podocarpus dubius sp. n.

FIG. 53. General aspect of both stomatiferous cuticles. Slide LP 225, ×100.

FIG. 54. A stoma. Slide LP 226, ×500.

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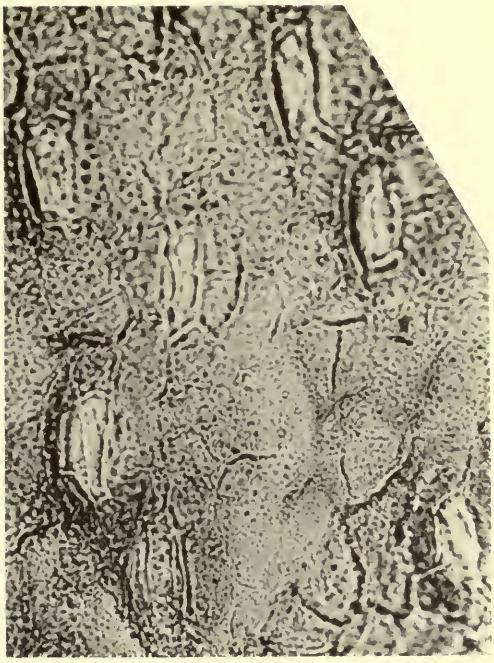

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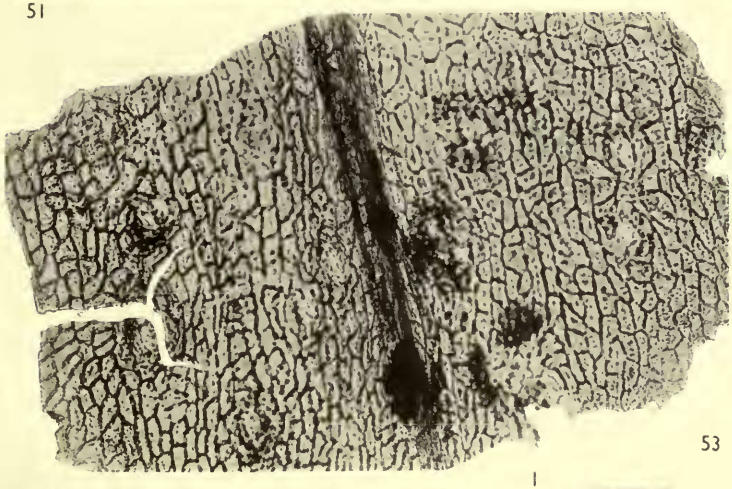

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PLATE 8

Trisacocladus tigrensis gen. et sp. n.

FIG. 56. Slightly macerated seed showing nucellus membrane and remnants of integument. Slide LP 156, ×30.

FIG. 57. Slightly macerated seed showing nucellus membrane and, on top, an oblique mark of enclosed megaspore membrane. Slide LP 157, ×30.

FIG. 58. Integument membrane showing small circular granules adhering to it. Slide LP 166, ×100.

FIGS. 59, 60. Pollen. The same specimen in equatorial view at two different focci, showing the exine patterns on the body and contracted air bladders of grain. Slide LP 54, ×1000.

FIGS. 61, 62. Pollen. Two specimens in equatorial view showing expanded air bladders. Slide LP 54, ×1000.

FIGS. 63–65. Pollen. Polar view of typical grains, showing three small air bladders. Slide LP 54, ×1000.

FIG. 66. Pollen. A grain in polar view. Slide LP 54, ×600.

FIG. 67. Pollen. A grain in equatorial view, showing three bladders. Slide LP 54, ×600.

Apterocladus lanceolatus gen. et sp. n.

FIG. 68. Pollen. Polar view, from cone LP 6296 (Slide LP 229). ×850.

FIG. 69. Pollen. Polar view from another cone, showing incipient 3 sacci. ×700.

FIG. 70. Pollen. Equatorial view showing thickened zone and thin distal exine. ×700.

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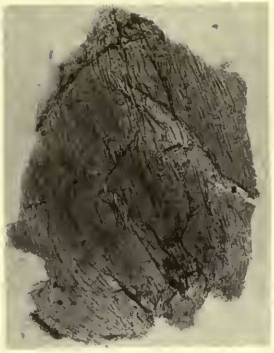
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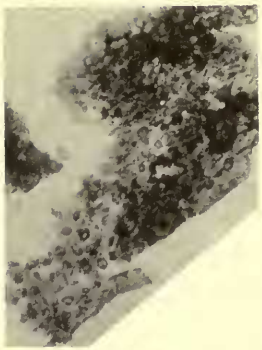
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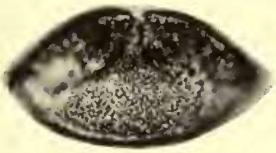
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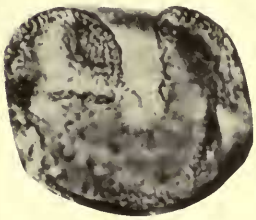
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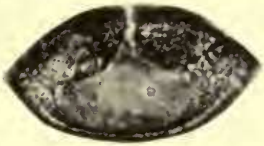
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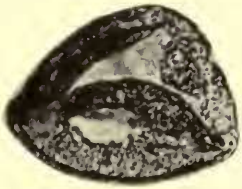
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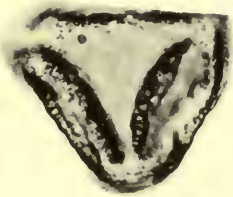
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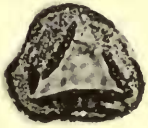
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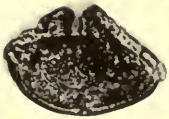
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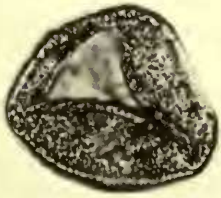
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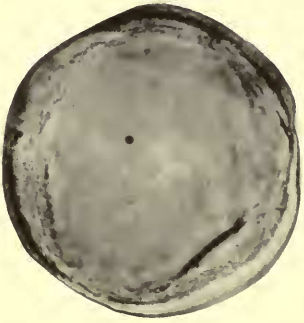
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